BIOLOGY, STATUS, AND MANAGEMENT OF THE TIMBER RATTLESNAKE (*CROTALUS HORRIDUS*): A GUIDE FOR CONSERVATION

WILLIAM S. BROWN

Society for the Study of Amphibians and Reptiles

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Cover drawing of a Timber Rattlesnake *(Crotalus horridus)* by Donald G. Wheeler, 2705 Sunset Trail Riverwoods, Deerfield, Illinois 60015.

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DEDICATION

The late and beloved

Bonnie Carver Brown
(21 June 1977 — 2 January 1987)

continues to give spiritually of herself to me, and this publication is dedicated to her memory.

Frontispiece of a Timber Rattlesnake (*Crotalus horridus*) from Richardson County, Nebraska, by John Lokke, P. O. Box 4382, Omaha, Nebraska 68104.

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INTRODUCTION

Early in 1990 I was approached by the Eastern Regional Office of The Nature Conservancy (TNC) to prepare, under contract, an Element Stewardship Abstract (ESA) for the Timber Rattlesnake (*Crotalus horridus*), the only wide-ranging woodland rattlesnake of the deciduous forest biome of eastern and central North America. The Nature Conservancy is an international ecological land conservation organization and is involved in conserving the Timber Rattlesnake by protecting lands where it occurs. The Conservancy began an ESA database to provide to state offices, Natural Heritage Programs, and private and public resource managers current management-related information in standard format and through a national computer system. As I got involved in the project on *Crotalus horridus*, I felt that there might be a broader need among conservation biologists, wildlife ecologists, and herpetologists for this information beyond the network of general availability of the ESAs. This publication is a result of that effort.

The Timber Rattlesnake seems always to provoke a great deal of interest and attention from those who are familiar with it in nature, and from those who exploit it. Knowing the snake in nature, however, does not automatically guarantee a willingness only to observe it there. Too frequently, a Timber Rattlesnake coiled quietly in its natural habitat is a target of wanton killing, and the snake has been heavily persecuted by bounty hunters and by collectors for the live animal trade. In at least one state (Pennsylvania), the snake is "taken" under a licensed sport hunting program, while neighboring states (New Jersey, New York) offer it full protection under state endangered and threatened species laws. A patchwork of lands, both public and private, often is administered with different approaches toward the presence of the Timber Rattlesnake. Many areas which afford it a last stronghold are under pressure of human incursions from expanding housing or "second home" developments, utility rights of way, and increasing rural roads and access.

I solicited help and input from a number of Timber Rattlesnake biologists and field observers among a fairly cohesive network of colleagues and collaborators. Many of them provided unpublished reports, as well as opinions and observations in correspondence, and agreed to be listed as experts for this species in their regions. Unfamiliar information, unquantified judgments, and unpublished preliminary observations are included. Intuition and "field sense" of those who know the Timber Rattlesnake are not omitted. This information has not previously been published but is often widely talked about among the network of workers on this species.

An ESA is designed purposely to be provisional and to provide for the continuous updating of information by conversant workers. This paper is, similarly, not a final statement of conservation needs of the Timber Rattlesnake.

It is, rather, an attempt to summarize current knowledge (most of the published older and current literature on the Timber Rattlesnake is also summarized and cited) and to point out areas where more research is needed. Much continuing effort by many people will be needed to revise, add to, and update this document.

DESCRIPTION

Similar Species

In areas where no other rattlesnakes of the genera *Crotalus* (rattlesnakes proper) or *Sistrurus* (pigmy rattlesnakes) occur, this snake may be distinguished by its rattle. The tail is relatively short and thick (see below) and its underside has a single row of transverse subcaudal scales (cf. double row, or divided subcaudals, possessed by sympatric harmless snakes of the family Colubridae). A facial pit, or hole in the side of the face, is present between the nostril and the eye. This pit gives the name "pit vipers" to the taxon which includes the rattlesnakes (subfamily Crotalinae, family Viperidae). The eye has a vertically elliptical pupil (cf. round pupil in sympatric colubrid snake species). The dorsal surface of the head is covered with many small scales, not a few enlarged scales or plates (cf. various colubrid species; *Sistrurus* species; Copperhead and Cottonmouth, genus *Agkistrodon*).

An excellent general treatment of snake identification, including a description of *C. horridus*, is in the field guide of Conant and Collins (1991). The facial pit, vertical pupils, and small head scales are illustrated by line drawings and labels in this field guide. Petersen and Fritsch (1986) and Rosenberg (1980) provide color photographs of harmless species commonly mistaken for the Timber Rattlesnake. Two of these species, the Eastern Milk Snake (*Lampropeltis triangulum*) and the Fox Snake (*Elaphe vulpina*), are slender and have skin that may be described as smooth, shiny, or glossy. In contrast, the Timber Rattlesnake is heavy-bodied with keeled scales; overall, a rattlesnake's skin appears coarse-textured, velvety, or dull. Two other species, the Northern Water Snake (*Nerodia sipedon*), and the Eastern Hognose Snake (*Heterodon platirhinos*), although having keeled scales, a dull texture, and a relatively heavy body form, lack the distinguishing characteristics of a rattlesnake, namely:

1. the short tail and rattle
2. single row of transverse scales on underside of tail
3. stout body girth
4. facial pit
5. small dorsal head scales
6. vertical pupils of the eyes.

All in all, there would seem to be little chance of confusing a Timber Rattlesnake with any of these four harmless species, but, lacking specimens for comparison, it does happen.

Adult Coloration and Pattern

Coloration and pattern of *Crotalus horridus* are highly variable geographically; this can present problems in identification. The ground color typically is yellow, gray, brown, or black. Four basic color morphs or variations are illustrated in Conant and Collins (1991), who describe them as (1) yellow variation, (2) black variation, (3) southern variation (also called the canebrake rattlesnake), and (4) western variation. Individuals showing much, but not all, of this intraspecific variation are in Figs. 1–16.

Adding a western variation to the third edition of the *Field Guide to Reptiles and Amphibians*, Conant and Collins (1991) helped clarify what, for many herpetologists, had been a source of confusion when attempting to identify specimens from populations generally west of the Mississippi River and north of the Ozarks (Figs. 1, 2, and 9). W. H. Martin (1990, pers. comm.) wrote: *"The failure to note the distinctiveness of the western morph causes a lot of confusion among not only amateurs but professionals. Amateurs from the western part of the range look at Conant's (1975) guide and call their snakes 'canebrakes' because western timbers often more closely resemble the canebrake morph than they do the yellow morph illustrated in Conant (1975). Western timbers are only very rarely a bright sulfur yellow, and the yellowish ones seem to be mostly from the north—Wisconsin and Minnesota. Usually they have a post-orbital bar* [cf. Storment, 1990] *and a mid-dorsal stripe. Ground color is buff* [reddish-yellow], *grayish-green, tan, or brownish. Bands are much more angular than the rounded bands of the eastern timber."* Martin (1992a) provides summary descriptions of the coloration and distribution of each of three forms he recognizes: the eastern Timber Rattlesnake, the western Timber Rattlesnake, and the southern Timber Rattlesnake. These three geographic variants correspond to those portrayed in Conant and Collins (1991). Martin's eastern Timber Rattlesnake comprises the yellow and black morphs.

The intraspecific classification of the Timber Rattlesnake is unstable. Some workers (Brown and Ernst, 1986) argue in favor of formally recognizing northern populations containing both the black and yellow morphs or other intermediate colorations (see below) as belonging to a northern subspecies, *C. h. horridus*, the Timber Rattlesnake. Others follow Pisani et al. (1972) in not giving formal subspecific recognition to either the northern variation or

to the southern variation, *C. h. atricaudatus* (Fig. 3). Technical descriptions of both subspecies are given by Gloyd (1940). Taxonomic arguments aside, there is striking variation within this wide-ranging species (Figs. 1–16). A comprehensive study of this color and pattern variation is needed.

An average of 24 (range 15–34) dark brown or black body blotches or crossbands or both occur dorsally from the neck to the base of the tail. Anteriorly, the dorsal blotches are separated from a lateral series of dark blotches by spaces of light ground color on the sides; at mid-body, these dorsal and lateral blotches tend to join to form complete crossbands often with a chevron shape. An earlier common name, "banded rattlesnake," alludes to these. The crossbands tend to become obscured by dark coloration posteriorly. The tail is a uniform dark brown or black. An early name of the species is "velvet tail" in reference to the tail's velvety-black appearance.

In mountainous areas from the Appalachians through the northeastern part of the range, many populations of *C. horridus* contain both yellow (Y) and black (B) morphs (Figs. 4, 5). Some yellow-morph individuals appear more brown than yellow (Fig. 6), but are distinguishable from black-morph snakes by head and venter coloration (below). Some black-morph individuals are patterned with blotches and crossbands on a dark grayish ground color. One color photograph of such a snake, apparently from Ohio, is in Rosenberg (1980), one from North Carolina or Virginia is in Martof et al. (1980), another from Kentucky is in Ernst (1992), and another of unknown provenance is in Behler and King (1979). These snakes belong to the black variation, as indicated by their head color, but they are more grayish or yellowish than are the typical black-morph snakes, with more prominent crossbands or blotches on a lighter ground color (Fig. 7). Still other black individuals show little evidence of banding and are nearly uniformly melanistic (Fig.8). Occasional individuals of both morphs have a faint dorsal rust-colored band down the midline of the back and separating the blotches and bands. Snakes of the western and southern variations usually show a prominent dorsal rust stripe (Fig. 9). In both Y and B individuals, the crossbands may be distinctly separated from the ground color by thin borders of narrow light yellow or white colored scales (Figs. 10, 11, 12). The color of the head of yellow-morph individuals is yellow or light tan (Fig. 13), that of black individuals is gray or black (Fig. 14). The underside of the head—the chin and neck—of the black morph is white, flecked with black; that of the yellow morph is yellowish to cream-colored, flecked with brown. The belly, or venter, of yellow-morph snakes is a uniform yellowish cream color, lightly flecked laterally with brown or black; the venter of black morph snakes is a black-mottled yellowish-gray or black-mottled light yellow. A summary of these characteristics follows:

Characteristic	*Yellow Morph*	*Black Morph*
Ground Color	yellow, tan	black, gray
Dorsal Bands, Blotches	dark brown, gray	black, dark gray
Dorsal Rust-Colored Band	occasional	occasional
Head, dorsal-lateral	yellow, tan	black, gray
Chin & Neck, ventral	light yellow	white; black flecks
Belly	yellowish cream	mottled yellow-gray
Tail	uniform black	uniform black

Illustrations

Line drawings of the dorsal pattern are in Babcock (1929), Breckenridge (1944), Brown and Ernst (1986), Green and Pauley (1987), Klauber (1956), Lang and Karns (1988), and Tyning (1990).

Line drawings of ontogenetic changes and sexual dimorphism in the postorbital bar (stripe from eye to angle of mouth) in a population from southern Illinois are given by Storment (1990). Generally, the postorbital bar is a characteristic found in the southern (canebrake) variation and in the western variation (cf. Conant and Collins, 1991), but is not found in the yellow or black morphs of northern populations (referred to the nominate subspecies, *C. h. horridus*; Gloyd, 1940).

References illustrating the species with black and white photographs, color photographs, or color drawings are:

Y and B variations: Allen (1992), Behler and King (1979), Brown (1987), Campbell and Brodie (1992), Conant (1938, 1947, 1975), Conant and Collins (1991), Ditmars (1944), Ernst (1992), Gloyd (1940), Martof et al. (1980), McCauley (1945), Palmer (1974), Petersen and Fritsch (1986), Pope (1946).

Y variation only: Barbour (1971), Conant et al. (1992), Ditmars (1929), Green and Pauley (1987), Klauber (1956), Klemens (1991), Linzey and Clifford (1981), Minton (1972), Pope (1946), Schmidt and Davis (1941), Surface (1906), Wright and Wright (1957).

B variation only: Huheey and Stupka (1967), Logier (1958), Reinert et al. (1984), Rosenberg (1980), Russell (1980).

Southern (canebrake) variation: Anderson (1965), Ashton and Ashton (1988), Campbell and Brodie (1992), Conant (1975), Conant and Collins (1991), Dundee and Rossman (1989), Ernst and Barbour (1989), Gloyd (1940), Holbrook (1842), Klauber (1956), Linzey and Clifford (1981), Mitchell and Schwab (1991), Mount (1975), Palmer (1974), Russell (1980), Tennant (1984, 1985), Wright and Wright (1957).

Western variation: Anderson (1965), Breckenridge (1944), Christiansen and Bailey (1990), Collins (1974, 1982, 1993), Conant and Collins (1991), Hudson (1972), Johnson (1987), Klauber (1956), Smith (1956), Smith (1961), Vogt (1981).

Aberrant pattern, albinism: Ditmars (1929), Hudson and Carl (1985), Nickerson and Mays (1968).

A recent book for youngsters by Lavies (1990) contains many excellent color photographs of *C. horridus*, and, along with its biologically accurate text, may be recommended as an introduction to this species for general readers of all ages.

Newborn Coloration and Pattern

At birth and prior to their neonatal molt, newborn are not distinctly recognizable as being yellow or black individuals in northern populations of Timber Rattlesnakes containing both Y and B color morphs. Baby *C. horridus* are best described as gray. After shedding, however, at an age of around 10 to 14 days, the morphs can be discerned more readily, particularly by head color (Figs. 15, 16). With growth and age, the color patterns increasingly diverge, showing considerable ontogenetic change. Within one year, yellow and black juveniles are clearly distinguishable.

Many newborn in northern Timber Rattlesnake populations have a distinct reddish-brown or reddish-orange band or stripe running along the entire mid-dorsal length of the snake. Neonates tend to show this trait more prominently than do adults. Newborn in southern (canebrake) populations, and in western populations, also have the mid-dorsal rust stripe, although B. L. Oldfield (1991, pers. comm.) says: *"Newborn timbers from Wisconsin and Minnesota are gray with black bands and tail, and they do not show middorsal stripes or postocular bars. The stripes and bars show up after the first ecdysis."*

Although the adults are frequently illustrated, such is not the case for the newborn. Photographs of newborn are in the following:

Campbell and Brodie (1992) (col.)—female and litter
Ditmars (1944) (b.& w.)—female and litter
Reinert (1985) (b.& w.)—female and litter
Petersen & Fritsch (1986) (col.)—pre-molt newborn with prebutton (neonatal skin cap at tail tip)
Brown (1987) (col.)—newborn shedding
Johnson (1987) (col.)—post-molt newborn with button (first rattle segment)

Size

No trait is more easily exaggerated than is the size of a Timber Rattlesnake. Most people seeing an adult *C. horridus* for the first time report its total length as between 4 feet (48 inches = 122 cm) and 5 feet (60 inches = 152 cm). However, even a 4-ft estimate is exaggerated for most Timber Rattlesnakes I have measured. Among males sampled in my ongoing field study, only 2.5% have been 4 ft. (122 cm) or longer in total length (W. S. Brown, unpubl. data).

To measure rattlesnakes, I use a "squeeze box" in which the compressed snake is measured along its natural curves using a calibrated map-measurer, a method of measurement first used by Galligan and Dunson (1979). This method reduces bias. Dead snakes, freshly shed skins, and living snakes forcibly extended for measuring are all subject to stretching.

Sexual dimorphism occurs in this species, with males being larger than females. Sex may be determined by the short tail in females vs. the long tail in males with virtually no overlap in adults. But in individuals less than 84 cm (33 inches) in total length, tail lengths of the sexes overlap. Geographic variation in body size occurs also, with southern (canebrake) populations averaging larger (cf. Gibbons, 1972) than northern (timber) populations. Average sizes of adults (males n=200, females n=150) and of neonates in northeastern New York are:

Males: Total Length = 111 cm (43.5 inches)
Tail Length = 9 cm (3.5 inches)
Weight = 900 g (2.0 lb)

Females: Total Length = 97 cm (38.5 inches)
Tail Length = 6 cm (2.5 inches)
Weight = 600 g (1.3 lb)

Newborn: Total Length = 31 cm (12.5 inches)
Weight = 20–25 g

Maximum size (total length) of the species accepted in the literature stems from an 1879 record of a 6 ft-2 inch (74 inches) (188 cm) specimen from New Jersey cited by Klauber (1956), and, more recently, the same size reported by Ditmars (1929) of a specimen taken in Massachusetts. Ditmars (1907) noted maximum sizes as follows: *"The writer's largest Pennsylvania specimen measured five feet and one inch in length. The largest specimen he has ever examined measured exactly six feet. This fine specimen was captured in Missouri."* Ditmars later (1929, 1944) cited his largest specimens of 6 ft-2 inches and 6 ft-0 inches, respectively, as both coming from "near Sheffield, Massachusetts" rather than from "Missouri."

W. H. Martin (1990, 1991, pers. comm.) notes: *"Strangely, most authors have uncritically accepted Ditmars' (1929) report of a 74-inch timber but they ignored his claim (Ditmars, 1944) to have measured two 8-foot canebrakes* [southern variants] *from Louisiana and a specimen 'a few inches over seven feet long' from South Carolina."* These sizes pertain to southern populations (referred to as the canebrake rattlesnake in Ditmars' and Martin's terms) which are known to attain a larger body size than northern populations (the eastern Timber Rattlesnake). Martin continues: *"In 1929 he reported a 6-foot 2-inch timber from Sheffield, Massachusetts. His 1944 book apparently refers to the same snake* [as a 6-foot 0-inch specimen], *but he carelessly failed to note what he had written the first time. I suspect he either estimated the lengths or failed to record them until long after the fact. Raymond Ditmars was unquestionably a good naturalist and an astute observer. However, the maximum lengths that he gave for snakes cannot be accepted unequivocally. I get the impression that he did not keep accurate field notes and that much of what he wrote was based on memory."*

Maximum size (total length) in *Crotalus horridus* may be eight feet (96 inches, or 244 cm) in the south, or 6-feet 2-inches (188 cm), or 6-feet 0-inches (183 cm), from either Missouri or Massachusetts in the north, depending on which of Ditmars' reports one is inclined to accept. Ditmars' record of a 61-inch (155 cm) specimen from Pennsylvania also should be considered. Gloyd's (1940) extensive study of museum material yielded maximum records of 61 inches (155 cm) in a Kansas female, and 51 inches (130 cm) in a Missouri male. Martin (1990, pers. comm.) says *"The longest authenticated eastern timber is in the Carnegie Museum* [Pittsburgh, Pennsylvania] *and is 59 inches* [150 cm]."

Unfortunately, some recent authors report the size of Timber Rattlesnakes as "lengths" without specifying whether total length or snout-vent length is meant, and without stating how the measurements were taken. Storment (1990), for example, gives a maximum length (presumably total length) of 146 cm (57.5 inches) among a sample of 14 males, and 121 cm (47.5 inches) for 17 females in southern Illinois. These snakes apparently were seen in the field, but methods of length measurement or estimation are not given.

In my 13-year study in New York and using the squeeze box and map measurer technique (1978–1990, W. S. Brown, unpubl. data), the largest animals were:

Largest Male: Total Length = 137.5 cm (54 inches)
Body Weight = 1,760 g (3.9 lb)

Largest Female: Total Length = 120 cm (47 inches)
Body Weight = 1,414 g (3.1 lb—gravid)

In captivity, growth may be greatly enhanced. I have raised two males from the same litter (female taken in southern Vermont by a snake hunter in 1981) which have achieved the following sizes after ten years (measurements recorded in October 1991):

Total Length = 142 cm (56 inches) (both specimens)
Body Weight = 2,477 g (5.5 lb) (B morph); 3,072 g (6.7 lb) (Y morph)

Along with depletion of many populations, the average body size appears to have undergone a reduction, probably because the larger snakes have traditionally been the easiest to kill and take, and because the extended time necessary for the snakes to achieve their natural longevities and maximum sizes is not available due to human predation pressures. W. H. Martin (1991, pers. comm.) says: *"I do not have any doubt that timbers ran bigger around the turn of the century. It is a simple matter of demographics. Not only were there more rattlesnakes but the proportion of old adults was much higher."* In most areas, workers today seldom report a specimen as large as 52 inches (132 cm) and a Timber Rattlesnake of this size is considered an impressive animal.

DISTRIBUTION

The current geographic range of *Crotalus horridus* encompasses 30 states from New Hampshire to Minnesota in the north, from extreme southeastern Nebraska and eastern Iowa to Texas in the midwest, across the south to northern Florida, and along the eastern coastal plain. Throughout its range, the species is perhaps most abundant where its denning colonies reach their highest densities: in the Appalachian Mountains from northeastern Alabama to Pennsylvania. Toward the northern and western fringes of its range, considerable isolation of surviving populations is evident as historical extirpation and habitat modification by humans have taken their tolls. W. H. Martin (1990, pers. comm.) states: *"The species is most abundant* [in population density] *in certain heavily wooded portions of the Coastal Plain from North Carolina to Louisiana."*

Detailed range maps are in Brown (1987), Collins and Knight (1980), and Gloyd (1940). General maps may be found in Conant and Collins (1991), Klauber (1956), and Wright and Wright (1957). The most detailed and regularly up-dated map available is by W. H. Martin (1992a), upon which the maps in Brown (1987) and Conant and Collins (1991) are based. State and regional maps include:

Alabama (Mount, 1975)
Connecticut (Petersen and Fritsch, 1986)
Florida (Ashton and Ashton, 1988)

Illinois (Smith, 1961)
Indiana (Minton, 1972; Richards, 1990)
Kansas (Smith, 1956; Collins, 1974, 1982, 1993)
Kentucky (Meade, 1991)
Louisiana (Dundee and Rossman, 1989)
Maryland (McCauley, 1945)
Minnesota (Breckenridge, 1944; Lang and Karns, 1988)
Missouri (Johnson, 1987)
Nebraska (Lynch, 1985)
New England (Kimball, 1978; Martin, 1982, 1992a; Petersen and Fritsch, 1986)
New Jersey (Martin, 1982)
New York (Martin, 1982)
North Carolina (Palmer, 1974)
Ohio (Conant, 1938, 1951; Wynn, 1991)
Oklahoma (Webb, 1970)
Ontario (Cook, 1984)
Pennsylvania (Martin, 1982; McCoy, 1982)
Texas (Dixon, 1987; Tennant, 1984)
Virginia (Linzey and Clifford, 1981; Martin, 1979)
West Virginia (Green and Pauley, 1987)
Wisconsin (Oldfield and Keyler, 1989; Vogt, 1981)

HABITAT

Wright and Wright (1957) tabulated more than 250 habitat names from various sources; among these, the descriptive terms *mountain* (39), *hill* (25), *ledge* (12), and *bluff* (12) were the most common. The species *"prefers oak lands, oak-pine woods, or oak-laurel-poplar-chestnut hills"* (Wright and Wright, 1957).

Some idea of geographic variation in habitat is indicated by the following geographic breakdown:

1. In the **northeast**, *"this species prefers remote mountainous terrain characterized by steep ledges and rock slides"* (Petersen and Fritsch, 1986) and *"timbered areas with rocky outcroppings, dry ridges, and second growth deciduous or coniferous forests...usually southern exposures"* (DeGraaf and Rudis, 1986) (see HABITAT IN NORTHEASTERN NEW YORK below.)
2. In the **upper midwest** the species occurs on steep rocky bluffs and bluff prairies with oaks (Breckenridge, 1944; Oldfield and Keyler, 1989; Vogt, 1981). In the **central midwest**, optimum habitats are

high, dry ridges with oak-hickory forests interspersed with open areas (Minton, 1972), and *"deciduous forest, especially along hilltop rock outcrops in thick woods"* (Fitch, 1958).

3. In the **south**, preferred habitat is *"hardwood forests of the type found in Loess Bluff and in many river bottoms"* (Cook, 1943), swampy areas and floodplains (Mount, 1975), wet pine flatwoods, river bottoms and hydric hammocks (Ashton and Ashton, 1988), upland pine, deciduous woodland, and sandy or black-clay riparian communities (Tennant, 1984), and hardwood forests and cane fields of alluvial plain and hill country (Dundee and Rossman, 1989).

Caution is recommended in interpreting habitat descriptions, as considerable geographic differences in slope, elevation, geological conditions, and plant communities clearly give each known Timber Rattlesnake area its own distinctive characteristics.

Many authors making observations of the snake's habitat as being steep and rocky do not distinguish the place where they hibernate (den, or hibernaculum) from the major area where the snakes move and forage (summer habitat). In addition, adjacent to the winter den, and located between it and the summer habitat, I recognize a third habitat type which I call "transient" habitat (see TRANSIENT HABITAT below). Thus, in mountainous country in the northern parts of its range, a distinction must be made between the habitat of *den sites*, *summer range*, and *transient areas*. A brief summary of these three habitat types follows.

DEN

A hibernaculum, or den, is typically located in a rocky area where underground crevices provide retreats for overwintering. In northeastern New York, granitic escarpments and ledges with accumulations of talus are prominent features at and around the sampled dens. Elevations of the dens are between 150 and 390 m (500–1300 ft). In the southern Appalachians, maximum den elevations are higher, at 1070–1430 m (3500–4700 ft) (Martin, 1992a). In the Pine Barrens of southern New Jersey, at elevations of 25–42 m (80–140 ft), Timber Rattlesnakes den along streams in white cedar swamps (Zappalorti and Reinert, 1992). In general, throughout the mountainous northeast according to the extensive survey work of W. H. Martin (1992b), a den typically will be one of three types:

1. *Fissure in a ledge*, or crevice interface between ledge and ground
2. *Talus* (*rock slide*) below a cliff, or open scree slope (fallen rocks not associated with a cliff)
3. *Fallen rock* (talus or scree) partly covered by soil

Some of the most colorful and still accurate descriptions of typical Timber Rattlesnake dens are in the writings of Ditmars and of Kauffeld. These authors described talus and fallen rock dens which are prevalent throughout much of the northern portions of the snake's range.

Ditmars (1942) said: *"A typical den is on the southerly slope of a hill or mountain of ledgy character. There may be a precipitous face of rock and at the bottom a jumbled mass of great fragments weighing tons. The spot denotes cataclysmic forces in action in dim ages past. Such forces have shattered the face of the cliff and among these shattered portions is a crevice at the bottom, or there may be several adjacent crevices. These form the den. The area is secluded and tangled. Wild grape writhes its way among the rocks."*

Kauffeld (1957) described a den as follows: *"The main part of the den consists of enormous rocks and boulders interspersed with smaller rocks, stones, and dead trees. Scrubby growth manages to gain nourishment and moisture from some of the leaf pockets, but Virginia creeper, wild grape and lichens are virtually the only plants that find the stones hospitable."*

Summer Habitat

Recently, two workers have published significant radiotracking studies that quantify—by multivariate statistical analysis using telemetric relocation data—the habitat in mountainous areas of Pennsylvania (Reinert, 1984a, 1984b) and in coastal Pine Barrens of southern New Jersey (Reinert and Zappalorti, 1988a). These studies have stressed that different sex and age classes of Timber Rattlesnakes have different habitat requirements. In southern New Jersey, males and nongravid females are primarily forest dwellers and use habitats with greater than 50% canopy closure, thick surface vegetation, and few fallen logs. In mountainous country in eastern Pennsylvania, males and nongravid females use canopied forests. In its wooded habitat, the Timber Rattlesnake is a sit-and-wait ambush predator of small mammals (Reinert et al., 1984; Brown and Greenberg, 1992b).

Using radiotelemetry, Brown and Greenberg (1992a) tracked four free-ranging adult *Crotalus horridus* (two males, two non-gravid females) in northeastern New York in 1991. Each time a snake was located, its body posture was recorded and structural habitat variables were measured after it had moved away from the location. Habitats at snake locations (n=63) were mixed deciduous or coniferous forests with canopy closure averaging 67%, and with most (nearly 60%) of the locations having greater than 75% canopy closure. Snake locations also were characterized by heavy fallen leaf cover, little surface vegetation, and few rocks or fallen logs. The most common overstory trees (n=143) at snake locations were Red Oak (*Quercus rubra*), Eastern Hemlock (*Tsuga canadensis*), Shagbark Hickory (*Carya ovata*),

Sugar Maple (*Acer saccharum*), White Ash (*Fraxinus americana*), White Pine (*Pinus strobus*), Beech (*Fagus grandifolia*), Hornbeam (*Ostrya virginiana*), Birch (*Betula* ssp.), American Basswood (*Tilia americana*), and Eastern Redcedar (*Juniperus virginiana*) (listed in order of decreasing frequency). Among 126 sightings of undisturbed Timber Rattlesnakes, the snakes were coiled out on the surface in 86% of our observations, and rarely were concealed under rocks or shrubs.

In contrast, gravid (pregnant) females used rocky, sparsely forested sites during their summers of gestation (Reinert, 1984b) and seldom fed. Gravid females used less densely forested sites with approximately 25% canopy closure, frequent fallen logs, and warmer climatic conditions (Reinert and Zappalorti, 1988a). Gestating sites for gravid females in Pine Barrens habitats frequently were the edges of sand roads. Similarly, in Wisconsin, Keenlyne (1972) reported gravid females using flat slab rocks and grassy, open slopes. This open habitat was not used by males or by nongravid females.

Most authors seem not to have recognized the distinction between the open, rocky situations near a den used by gravid females, and the forested summer habitat distant from a den used by nongravid females and males. But, referring to rocky ridges in Indiana—and seemingly anticipating these results—Minton (1972) says *"...the snakes show no preference for cliffs, ledges, or other massive rock outcrops, indeed they seem to avoid such places."*

Transient Habitat

I have found it useful to recognize "transient habitat" as a habitat type distinct from the den and summer-range habitats. Transient habitat is named for the ephemerality of snake movements through it, as implied in the first usage of the term by Ditmars (1942). Both in definition and in recognition in the field, this habitat is somewhat arbitrary. Generally, it is "close-in" habitat located within 200 m of a den. It tends to be broken by the rough topography and rocky terrain near the den site and supports more open woodland with exposed clearings and shelter rocks.

In July and August 1985, relative coverages in transient outcrop knoll habitats in northeastern New York were sampled on 25 1-m^2 plots at several representative sites (W. S. Brown, unpubl. data). Relative coverages were:

grasses, 41%;
rock surface including lichens and mosses on rocks, 19%;
leaf litter and branches, 16%;
trees and shrubs, 14%;
lichens and mosses not on rocks, 9%.

Transient habitat occurs on outcrop knolls used as "stop-over" basking locations by rattlesnakes migrating away from a den in spring or toward it in autumn. Timber Rattlesnakes are known to use specific shelter rocks which seem to be preferred and are frequented year after year. The snakes find and use these rocks typically during their close-in migrations. Such rocks may be preferred by the snakes because they provide certain physical requirements or protection for the snakes (see BEHAVIORAL DISTURBANCE BY HUMANS below).

Transient habitat also is used by adult females during their reproductive years. It is here that these females are vulnerable during their summers of gestating and birthing. If an area is subjected to sport hunting or commercial collecting, most snake hunters during the summer will be successful in finding only pregnant females, usually in transient habitats.

In a study of impacts of organized Timber Rattlesnake hunts in Pennsylvania, Reinert (1990) found 84% of females turned in by snake hunters were gravid. He states: *"Pregnant individuals have a greater susceptibility to being captured by hunters than their non-pregnant counterparts. This is undoubtedly a result of the preference of pregnant* C. horridus *for more open, rocky habitats than non-pregnant females."* More than any other factor, human exploitation with its high take of reproductive females has led to the recent depletion or collapse of many populations of *C. horridus* (see SPORT HUNTING AND ORGANIZED ROUND-UPS below).

HABITAT IN NORTHEASTERN NEW YORK

One region under study in northeastern New York (Brown, 1992b) is an area probably typical, in many respects, of the snake's habitat in the northern portions of its range. Latitude of the study area in northeastern New York is between 43 and 44 degrees north; elevations range from 98–688 m (320–2256 ft). The area is within the hemlock-white pine-northern hardwoods subregion of the cold temperate (boreal) conifer-deciduous forest (Greller, 1988). Forest communities in the mountains around the study site are dominated by Eastern Hemlock (*Tsuga canadensis*), Beech (*Fagus grandifolia*), and Sugar Maple (*Acer saccharum*).

Near rattlesnake dens, habitats are more open as local geologic and physiographic conditions—chiefly steep slopes, rock outcrops, and shallow soils—prevent the vegetation from reaching its regional potential. Well drained oak-hickory woodlands, grassy shelf clearings, and lightly wooded outcrop knolls occur on moderately steep, generally south-facing slopes. These habitats usually contain boulders, slab rocks, and outcrop fissures which provide ideal cover and microhabitat for Timber Rattlesnakes. Fitch's (1982) description of *C. horridus* habitat in Kansas applies well to the clearings and outcrop knolls in northeastern New York: *"Deciduous forest,*

especially of open type, with dry, rocky areas and rugged terrain."

Outcrop knolls and shelf clearings are used by most snakes migrating to and from the dens in September and May, respectively, and these areas are, therefore, called transient habitats. Besides providing migratory routes, outcrop knolls are also used by gravid females as primary sites for gestation in summer (see TRANSIENT HABITAT above). All other age/size classes of *C. horridus* (adult males, nongravid females, juveniles and subadults) generally move through the transient areas and reach their summer ranges in more distant canopied deciduous forests well removed from the vicinity of the dens (see SUMMER HABITAT above).

Vegetation composition of outcrop knolls in northeastern New York is reported by Brown (1992b). Typically, these knolls contain mixed communities of Red Oak (*Quercus rubra*), Shagbark Hickory (*Carya ovata*), Hornbeam (*Ostrya virginiana*), Sugar Maple (*Acer saccharum*), White Pine (*Pinus strobus*), Black Cherry (*Prunus serotina*), Red Maple (*Acer rubrum*), White Ash (*Fraxinus americana*), Common Juniper (*Juniperus communis*), Staghorn Sumac (*Rhus typhina*), and Eastern Redcedar (*Juniperus virginiana*) (listed in approximate order of decreasing abundance). Ground shrubs are chiefly Downy Arrowwood (*Viburnum rafinesquianum*), Serviceberry (*Amelanchier* sp.), and Blueberry (*Vaccinium* sp.).

Reschke (1990) describes "Appalachian oak-hickory forest" in New York which is similar in composition to that described above. This plant association appears to characterize a community type inhabited widely by *C. horridus*, and is described as follows: *"A hardwood forest that occurs on well-drained sites, usually on ridgetops, upper slopes, or south- and west-facing slopes. The soils are usually loams or sandy loams. This is a broadly defined forest community with several regional and edaphic variants."* A second plant association, "Acidic talus slope woodland" is identified as including the Copperhead (*Agkistrodon contortrix*) and the Timber Rattlesnake as characteristic animals. This community is scattered throughout upstate New York and is described as *"an open to closed canopy woodland that occurs on talus slopes composed of non-calcareous bedrock such as granite, quartzite, or schist"* (Reschke, 1990).

ECOLOGY

DENNING

In the colder climatic zones and mountainous areas in the northern parts of its range, a Timber Rattlesnake population is defined by its den. The den is central and critical to the viability and survival of an entire population. Early naturalists observed that rattlesnakes behaved as if they "knew" their home

den. Statements such as the following are in the literature of the early 20th century: *"They appear to find the same places, year after year, making their way from the adjoining timber and lesser ledges as if led by some strange, instinctive power"* (Ditmars, 1907). The modern phrase *communal denning* describes this phenomenon.

In mid-latitude and southern regions, some workers have questioned whether denning is prevalent. Tom R. Johnson (1991, pers. comm.) notes: *"In southern Missouri, and I presume elsewhere,* Crotalus horridus *does not den up. We have no reports of any possible dens where they congregate as they do in central and northern Missouri. Where do they go? How do they get together to mate? Has anyone studied these 'non-denning' populations?"* Anderson (1965), however, referred to *"large denning aggregations"* of the canebrake rattlesnake (southern variant) in southeastern Missouri, and Neill (1948) believed communal denning occurred in limestone caves in the Savannah River swamp of northeastern Georgia, so in some regions, at least, the existence of communal denning appears enigmatic and still needs to be carefully documented.

In recent years, several studies involving radiotelemetric tracking and lab experiments have documented the snakes' movement patterns and home range sizes, and have suggested possible mechanisms of orientation and den location (Brown and MacLean, 1983; Reinert and Zappalorti, 1988a, b). These studies have taken place in the north where communal denning occurs. In the southernmost portions of its range, where communal denning probably does not occur, the species has as yet not been similarly studied.

Spatial Biology

Timber Rattlesnakes are migratory. Seasonal migrations occur in two phases: (1) moving away from the den in spring (out-migrations), and (2) moving toward the den in autumn (in-migrations). The snakes' migratory movements take them into forested uplands, distant ridges, and—to a lesser extent—into lowland valleys and cultivated areas. These summer movements sometimes are surprisingly long, bringing snakes into areas where their occurrence is unexpected. Distances moved by individuals obviously must be known in order to protect an adequate area of summer range habitat (see Land Protection below).

The most thorough studies to date on movements and spatial biology are those of Reinert and Zappalorti (1988a) in the Pine Barrens of southern New Jersey, and Reinert (1991b) in deciduous woodlands of eastern Pennsylvania. Mean sizes of activity areas, or home ranges, in these areas are as follows:

	New Jersey	Pennsylvania
Males	207 ha (511 acres)	65 ha (160 acres)
Females, nongravid	42 ha (104 acres)	17 ha (42 acres)
Females, gravid	22 ha (54 acres)	4 ha (9 acres)

Pine Barrens rattlesnakes migrated an average of just over 1 km (0.6 mile) from their den and tended to move in a looping pattern away from, and then back toward, the den. Details of shedding, foraging, and mating behaviors affecting the snakes' movements are in Reinert and Zappalorti (1988a). Martin (1992b) records a maximum migratory distance of 6 km (3.7 miles) from dens in the Appalachian Mountains of Virginia. Usually, however, snakes (both sexes, all age/size classes) in that region move mean distances of 1.0 to 1.3 km (0.6 to 0.8 mile) from dens (Martin, 1992b). In northeastern New York (W. S. Brown *in* Macartney et al., 1988; Brown, unpubl. data), migration movements are as follows:

Mean maximum migratory distance from den:
Males 4.07 km (2.5 miles)
Females, nongravid 2.05 km (1.3 miles)

Maximum single migratory movement from den:
Male 7.2 km (4.5 miles)
Female, nongravid 3.7 km (2.3 miles)

It has been established that gravid females preparing to give birth in September (the usual month of parturition) move the least, both in migration distance from their den and in size of summer range (Brown et al., 1982; Galligan and Dunson, 1979; Keenlyne, 1972; Martin, 1992b; Reinert and Zappalorti, 1988a). Gravid females also have special habitat requirements during their summer of gestation (see TRANSIENT HABITAT above).

One mechanism of locating a den by adults and neonates has been suggested to be scent-trailing. Presumably this involves one snake using its olfactory (vomeronasal and nasal) senses to smell the odors of a chemical trail from skin secretions of another individual. Brown and MacLean (1983) reported experimental evidence in laboratory tests that newborn can follow scent-trails of adults. Recently, Reinert and Zappalorti (1988b) presented strong observational evidence, based on telemetric field tracking, that newborn Timber Rattlesnakes follow the scent-trails of adults in nature.

SEASONAL CYCLE

The Timber Rattlesnake, as an ectothermic reptile, undergoes a definite annual cycle related to seasonal changes of temperature in its environment.

Thermoregulation and winter survival require most populations to undergo a period of hibernation through the winter. In the northern half of its range and in mountainous areas, the period of winter dormancy is longer than in the southern portions of the range, but in nearly all areas where it occurs, the species alternates seasonal warm-weather activity with cold-weather inactivity, or hibernation.

Major phases of the seasonal cycle recognized here are:

1. *Earliest Emergence*—First appearance of a rattlesnake on the surface of a den in spring;
2. *General Emergence*—Range of dates encompassing the bulk of rattlesnakes appearing on the surface of a den in spring;
3. *General Ingress*—Range of dates encompassing the bulk of rattlesnakes appearing at a den in the autumn;
4. *Latest Ingress*—Last appearance of a rattlesnake on a den in the autumn.

The seasonal cycle may be summarized as follows in two areas (western VA, northeastern NY) where the species has been studied over a number of years by Martin (1992b) and Brown (1992b), respectively:

	Virginia	*New York*
Earliest Emergence	8 March	8 April
General Emergence	18 April - 12 May	7 May - 21 May
General Ingress	1 Oct - 21 Oct	14 Sept - 1 Oct
Latest Ingress	5 Nov	16 Oct

Geographic variation in the seasonal cycle is pronounced. Latitude and elevation affect the timing and length of the major phases of the cycle. In the south, *C. horridus* has a longer active season (late spring, summer, and early autumn) than a hibernating season (Martin, 1992a), whereas in the north the hibernating season exceeds the active season in length. In northeastern New York, the Timber Rattlesnake hibernates typically for 7.4 months and has a 4.6-month active season (early May through late September) (Brown, 1992b).

Reproductive Biology

Early work on two other species of North American rattlesnakes (*Crotalus atrox*, *C. viridis*) showed females reproduced at two-year intervals. Such a pattern, known as a biennial reproductive cycle, was assumed to occur in *C. horridus* and was reported by Gibbons (1972) in South Carolina, Keenlyne (1978) in Wisconsin, Galligan and Dunson (1979) in Pennsylvania, and Fitch (1985) in Kansas. Others, particularly Martin (1988), reported that most

females he had marked and recaptured after several years were reproducing at three-year intervals.

Age of first reproduction in females has been reported in several studies as follows: 4 years in Wisconsin and Kansas (Keenlyne, 1978; Fitch, 1985), 5 years in Pennsylvania (Galligan and Dunson, 1979), and 6 years in South Carolina (Gibbons, 1972). Martin (1988) reported females in Virginia bear first litters at ages of 5 to 9 years.

Litter size varies geographically. As summarized by Fitch (1985b), data on litter sizes (mean, range) are:

northeastern (New York)—9.3 (4–14)
northwestern (Wisconsin)—8.4 (3–11)
west-central (Kansas)—8.5 (5–14)
southeastern (South Carolina)—12.6 (10–16)

A combined picture of the reproductive pattern in this species is low-frequency birthing and delayed age of first reproduction. Recently, data collected by Brown (1991) by recapturing marked females over a period of eleven years (1978–1988) in northeastern New York show an even greater extreme in this pattern than had been reported in earlier studies. These findings are as follows:

Reproductive Cycle Length		*Age of First Reproduction*	
2-year cycle	0% of sample	6 years or less	0% of sample
3-year cycle	57% of sample	7 years	10% of sample
4-year cycle	27% of sample	8 years	16% of sample
5-year cycle	13% of sample	9 years	22% of sample
6-year cycle	3% of sample	10 years	39% of sample
		11 years	13% of sample

Brown (1991) found no evidence of a biennial cycle in the northeastern New York population, but rather discovered that females typically reproduce only every three or four years. These data confirm that the Timber Rattlesnake is a slow-reproducing species in its northern localities. The species also is long-lived compared to many other squamate reptiles: maximum recorded longevity in captivity is 30 years (Snider and Bowler, 1992).

Summarizing his findings, Brown (1991) stated: *"It may be reasonable to propose a schedule typical of a female in northern populations of* C. horridus *as follows: first reproduction at age 9 and triennial pregnancies thereafter. Such a female might have as few as three to five lifetime reproductive events lasting over a span of 7 to 13 years, or to an age of some 16 to 22 years. [Some Timber Rattlesnakes may exceed these ages, however; based on rattle sizes*

and appearance of "old-looking" animals, maximum longevity could extend possibly to 25 years.] These demographic traits are the main reasons why recovery of depleted populations will be slow."

It should be noted that, as in morphological characteristics and in habitat, life history characteristics vary geographically. With longer active season lengths and warmer climates, southern and western populations of *C. horridus* may grow faster, mature earlier, and reproduce more frequently than do northern populations. There is an indication also that litter size is larger in southern than in northern populations. More research is needed to compare these demographic traits at different latitudes.

Demography

Detailed quantitative population studies of the Timber Rattlesnake have not been published. Several workers are accumulating data toward this end (e.g., Brown, unpubl. data; Fraser and Fritsch, 1992; Martin, 1991). Based on the population biology of long-lived species of reptiles and their vulnerability to sporadic collecting (Harding, 1991), reasonable predictions may be made about the general life history strategy of the Timber Rattlesnake. From the outlines of this model, impacts on a Timber Rattlesnake population may be inferred.

The Timber Rattlesnake has the following life history characteristics:

1. Long natural lifespan (approximately 25 years).
2. Low reproductive rate.
    1) Females reproduce at three-year and four-year intervals (north), or at two-year intervals (south-midwest).
    2) First reproduction in females at ages of seven to eleven years (most commonly at nine and ten years) (north), or at ages of four to six years (south-midwest).
    3) Small litter size (usual range six to nine young, north; ten to fourteen young, south-midwest).
3. Stochastic (probabilistic) reproductive events.
    1) Highly variable reproductive performance, with climatic factors altering or damping cyclical patterns of female reproduction (all areas).
    2) Infrequent reproductive attempts in a lifetime (possibly three to five reproductive attempts for most females in northern populations).
4. High mortality in juveniles (low survivorship).
5. Low mortality in adults (high survivorship).

Reproductive frequency in *C. horridus* is variable as climatic factors modify or shift the occurrence of the triennial or quadrennial cycles, producing a series of low-reproduction years punctuated occasionally by high-reproduction years. This phenomenon has been documented by W. H. Martin (1993) who describes the climatic influence as causing "synchronization" of the reproductive cycles. Densities also may fluctuate in long-term cycles along with a variety of annual environmental factors. These patterns may be difficult to observe in typical short-term studies. In my field work during the past decade (1981–1991) of continuous study and monitoring of one metapopulation containing several contiguous dens, I have detected no noticeable population increases.

The Timber Rattlesnake is a species in which there apparently is little natural "harvestable" or "expendable" surplus of adult individuals. Populations are characterized by stability, and probably by a predominance of older age classes, little annual turnover, and variable annual recruitment. The impact of removing a single adult animal from a population with this life history pattern would be relatively high. Although population growth rates would be low, depleted populations of Timber Rattlesnakes, if left alone, do have the capability of recovering (see RECOVERY POTENTIAL below).

Given that most *Crotalus horridus* populations already have been depleted by human activities (see THREATS below), additional human-caused mortality factors impinging on populations of this species are significant in that they very likely are able to inhibit obvious numerical expansion. In Pennsylvania, where snake hunting is widespread, Smith et al. (1991) conclude: *"Because of selective pressure on pregnant females from summer snake hunting around the dens, most populations are heavily skewed in favor of males with less than 25% having what we consider to be viable populations of at least 8–10 reproductive-age females."* Even without snake hunting, the current rates of human-caused mortality in most areas (chiefly incidental but deliberate killing or collecting, and highway mortality) are high enough to prevent any measurable population increases in this species.

POPULATION TRENDS

No careful mark-recapture population estimates have yet been published for *Crotalus horridus*. One long-term study (W. S. Brown, northeastern New York) will provide such estimates after several more years of field work. What has been clear to date is the difficulty of recapturing individuals other than gravid females regularly. This problem may cause violation of an important sampling assumption of equal catchability of all sizes and age classes, an

assumption necessary for population estimates to be valid (Krebs, 1989). I have recaptured some snakes after long lapses (up to ten years) and it remains to be seen how the problem of inconsistent recaptures will affect calculations.

From earliest settlement of the North American continent, hunting rattlesnakes at their dens became a regular habit of many pioneers (cf. Adler, 1961; Palmer, 1992). Babcock (1929) commented: *"It is probably only a matter of time when the Timber Rattlesnake in New England will share the fate of the passenger pigeon."* In fact, *C. horridus* has been extirpated from two northeastern states in which it formerly occurred: Maine in the 1860s (Hutchinson and Hunter, 1992), and Rhode Island in the 1970s (Raithel, 1992). Vermont's stocks have been reduced from approximately 25 known historical sites to only two viable colonies today (DesMeules, 1992). In a fourth New England state, New Hampshire, the species' status is precarious and it may well be on the verge of extirpation there (Taylor and Soha, 1992).

The first major recent warning was published by Galligan and Dunson (1979) who, on the basis of counts of snakes turned in by snake hunters and on interviews with them at a number of local community-sponsored rattlesnake hunts in Pennsylvania, documented severe declines in Timber Rattlesnake numbers. Stechert (1982) summarized factors in the historical decline of this species in New York. Brown (1984, 1988) suggested denning populations in New York have been reduced by 50 to 75% of their historical numbers. Martin (1982) stated that most long-term observers feel that most Timber Rattlesnake dens are at 15% to 20% levels compared to forty years ago.

Recognizing the scarcity of objective data by mark-and-recapture methods to show trends in numbers, an overall consensus among virtually all scientists and field observers is that the Timber Rattlesnake indeed is declining over most parts of its range. Following a symposium "*Conservation of the Timber Rattlesnake in the Northeast*" held in December 1991, Thomas F. Tyning, a naturalist with the Massachusetts Audubon Society (sponsors of the symposium), summarized the snake's regional status: *"The Timber Rattlesnake is in worse shape than I believed. Others I spoke with recently agreed, especially here in the northeast. It is apparently extirpated from both Maine and Rhode Island and is close to the same in New Hampshire. The remaining populations in Vermont, Massachusetts, and Connecticut are under major and accelerating threats from private collectors, construction projects, habitat destruction, and fragmentation of habitat. New York and New Jersey populations, once thought to be the stronghold in the northeast, have been reduced by alarming percentages* [see below]. *Information provided by biologists from Ohio* [Wynn, 1992], *Minnesota* [Keyler and Oldfield, 1992b], *and elsewhere on the northern edge of the Timber Rattlesnake's range indicate serious depredations in the past and only relict populations remaining"* (Tyning, 1992).

In perhaps the most thorough long-term regional survey in existence, Stechert (1992) provides a recent state-wide den status summary for New York and northern New Jersey: *"Data on localities and population status were compiled from 139 extant dens in New York and 21 extant dens in northern New Jersey. Of the estimated total of existing dens, known dens represent approximately 90% of the dens in New York and approximately 95% in northern New Jersey. An additional 51 extinct dens are tabulated. Among all dens known historically in New York, 26% (n=49) are now extinct and another 5% (n=9) face imminent extinction. In the sample of 139 active dens surveyed in New York, 76% are in various stages of depletion, ranging from moderately depleted to critically depleted. Only 24% of the dens have relatively undisturbed (average) populations, and only 5% of the dens contain large populations by today's standards."*

Against this background, there are some den population estimates that have been made "informally," or venturing an estimate based on intuition, by several workers who have considerable field experience studying or observing the species. Required in this approach is some sense of the Timber Rattlesnake's overall proclivity to remain hidden underground and under rocks. Generally, most experienced field workers (W. S. Brown, W. H. Martin, S. H. Harwig, R. Stechert) seem to feel that under ideal weather conditions at dens in spring, 25% is about as large a proportion of the snakes that might be visible on the surface at any one time in any one place. Martin et al. (1990) used a smaller proportion in their field surveys, estimating that during peak spring emergence usually only 5% to 15% of the population may be seen. This is an estimate of the proportion of the snakes which happen to be in sight due to their using the surface part of their vertical microhabitat. Subjectivity and some error are inherent in this approach, but it is better than no estimate.

Estimates of population sizes of dens have been made in several areas using a combination of the estimated proportions of the snakes visible on the surface, and repeated observations over a sampling period of several years. In their recent extensive survey of the Timber Rattlesnake in Pennsylvania, Martin et al. (1990) state: *"We believe that with two to four visits per year over 4 to 5 years it is possible to fairly accurately estimate the population of a den colony."* Their survey of known dens where they have seen rattlesnakes in Pennsylvania over approximately the past fifty years yielded the following estimates (Martin et al., 1990):

Den Population Estimate (Number of Rattlesnakes)	Number of Dens	Percentage of Dens
0–15	78	25.6
15–30	117	37.5
30–60	72	23.0
60–120	37	11.9
>120	8	2.6

Martin et al. (1990) state: *"The mean estimated present population per den for the 312 dens at which we have seen rattlesnakes in Pennsylvania is 36 snakes per den. Only 25% are believed to have populations of 45 or more snakes (the minimum size that we would consider viable)."* A further analysis of the Timber Rattlesnake's predicament in Pennsylvania and the findings of the Martin report (Martin et al., 1990) appears below under SPORT HUNTING AND ORGANIZED ROUND-UPS.

In relatively unexploited areas, or where the snakes have not been subjected to recent hunting pressure, den sizes seem to be larger than are suggested above for exploited areas. In northeastern New York, the largest two dens contain an estimated 150 and 200 snakes each; most of the others have populations estimated at 40 to 100 animals each (W. S. Brown, unpubl. data). For comparison, Martin (1992b) has provided similarly-based estimates of den sizes in the Appalachian Mountains of Virginia. The two largest dens are estimated to have populations of 150–200 snakes, and ten of the largest dens (among more than 180 dens sampled) have approximately 120 snakes each. A majority of the dens are believed to have populations ranging from 30 to 60 snakes each (Martin, 1992b).

DETERMINATION OF OCCURRENCE

Occurrence of the Timber Rattlesnake on a site depends on the presence of an active den. If a den is on the site, then monitoring it at appropriate seasons will provide a basis for a quality rating of the area based on the den's estimated size. If a den is off the site, but the site includes summer range habitat used by rattlesnakes migrating to it from a distant den, other standards are appropriate. The following criteria should be used in evaluating the snake's occurrence in each situation.

DEN ON-SITE

1. *Spring Sampling.*—Counts of rattlesnakes seen on or near a den should be made at three-day intervals for about a three-week period during the snakes' peak emergence period in April or May (peak emergence varies with latitude and elevation). A healthy den (40 to 100 individuals) should produce roughly 8 to 15 individuals seen on at least several days.

2. *Summer Sampling.*—Counts of gravid females may be made in July and August in transient habitat near a den (see TRANSIENT HABITAT above). Although the frequency of females that are reproductive varies widely from year to year (for example, from 25% to over 75% were gravid among annual catch samples reported by Brown, 1991), at least several gravid females should be seen.

Data illustrating this approach are outlined as follows. One den of about 125 snakes (all age/size classes) estimated intuitively and observed annually for ten years has yielded between 3 and 5 gravid females consistently each year (W. S. Brown, unpubl. obs.), or perhaps 20 to 25% of the approximately 15 to 20 adult females that are believed to be present in this den population. Arriving at a crude population estimate in this manner assumes two levels of proportional reductions, that of surface visibility and that of the annual fraction of mature females reproductive. In conducting visual sampling at such a den area, approximately four or five mid-summer visits might be made, at weekly intervals or longer, to achieve a reliable count of gravid females. In the example given, estimating the den population by mark-and-recapture methods has yet to be done, so independence between the two methods cannot be stated with certainty.

Den off-Site

1. *Summer Sampling*.—Sampling summer range habitat used by migratory snakes from a den up to two miles distant will not prove to be reliable by standard snake-searching methods. Only occasionally will a rattlesnake turn up, usually coiled out in the woods. But if spots occur that attract rattlesnakes, it is usually worth checking them. Sites such as rocky outcrop clearings, rock walls along roads or fields, rock piles, quarries, and cleared spots in housing developments are good candidates for locating a rattlesnake on summer range. Because of annual variation in their use by rattlesnakes, however, these sites will require a four-year to five-year period of monitoring to provide the researcher with an estimate of relative abundance. Even then, the estimate will not be as reliable as estimates obtained from spring or summer den-on-site sampling (above).

2. *Interviews with Local Residents*.—In the northeast, and probably in many other places, most areas of occurrence of viable Timber Rattlesnake dens are well known and have been well known for generations. It is therefore worthwhile asking local people if they occasionally or regularly see (or kill) any rattlesnakes. If their residences are within rattlesnakes' summer migratory range, at least one local resident probably will report that people do see or kill them. About three or four separate residents living in proximity to suspected rattlesnake range should be interviewed, and, if all report no sightings, very likely no rattlesnakes exist in the region.

THREATS

Reviewing the status, conservation, and management of snakes, Dodd (1987) provided designations of major threats to the Timber Rattlesnake as

follows: (1) collection for use as pets, and (2) malicious killing. Among all pitvipers worldwide (approximately 144 species; Campbell and Brodie, 1992), more than half (80 species) are identified as vulnerable to extinction (Greene and Campbell, 1992). Several categories of threats to the Timber Rattlesnake are summarized below.

Habitat Destruction

Many stories told by experienced rattlesnake observers relate callous actions against the snake's habitat taken by some prior human. These disruptions most often involve moving a rock in search of a Timber Rattlesnake beneath it. Many years and even decades later the scars of a moved rock may be seen.

R. Stechert's surveys and observations (1981; 1991 pers. comm.) of New York Timber Rattlesnakes have revealed considerable habitat disturbance: *"All of the dens mentioned have been exposed to depredations by either snake hunters, hunters, hikers, loggers, or other people involved in work or recreation outdoors. I have found shotgun shells in or near several dens and summer basking areas, and have occasionally seen saplings, cut and used as prying poles, lying around displaced shelter rocks. Repeated disturbance of favored basking and shelter rocks will cause the snakes to temporarily abandon these sites. If the rocks are continually repositioned, as when pry poles are used, the snakes may stop using them altogether."*

A serious problem in Pennsylvania is malicious destruction of habitat by snake hunters. Stephen H. Harwig, perhaps the dean of long-term observers, has done extensive survey work throughout Pennsylvania rattlesnake country for over fifty years and has written thousands of pages of detailed notes on his observations of *C. horridus*. He says: *"Most of my friends hunt as I do. We cover miles of rough mountain country, see from none to several dozen rattlers, bring back the usual catch, zero. We enjoy the scenery and the census-taking. We're doing our part in leaving the wilderness alone. But we're leaving it for the other fellow. We can cite case after case, especially in the last few years, where we see hardly any rattlers where we used to see 5 to 25. We see more cut snake sticks and broken and dislocated rocks. Rocks are pushed off ledges, turned over by crowbars or pry poles, blasted with dynamite, or purged underneath by railroad flares or man-made fires. Sometimes the only evidence of recent hunting in a little-hunted den is a foot print, broken brush, a crumpled cigarette pack, slightly moved rocks, rifle or shotgun shells, or unusual scarcity of snakes seen* [by us]" (S. H. Harwig, 1981; S. H. Harwig pers. comm. to C. J. McCoy, 15 Feb. 1977).

Human Incursions into Rattlesnake Range

If an animal's place of residence is usurped, clearly this can have as devastating an effect as scattered destruction of primary habitat. In states where the snake is legally protected (New York, New Jersey, Connecticut, Massachusetts, Vermont, New Hampshire—see State Laws below), pressures of human population expansion into areas very near rattlesnake dens, usually for housing developments, are beginning to cause a major problem. Human incursions from rural "second-home" and condominium construction, along with their roads and golf courses, are threatening the Timber Rattlesnake in some areas of the northeast particularly. In several places, individual landowners are building houses in prime habitats near rattlesnake dens. There is no doubt that modern real estate development is currently posing a considerable threat.

One rattlesnake area in central Connecticut has recently been degraded by real estate development. In the mid-1980s a builder cleared 48 acres of woods, orchard, and meadows which are part of the snakes' summer range. Some of the prospective human residents were hostile to Timber Rattlesnakes and called for their extermination or removal (R. W. Fritsch II and D. F. Fraser, pers. comm.; Fritsch, 1992). In addition to new human residents, land developers are inclined toward intolerance to rattlesnakes and generally are not sensitive to the need for mitigation steps designed to protect rattlesnakes in new housing areas.

In contrast, another area in northeastern New York is used both as a study area for population research on the Timber Rattlesnake and as a vacation area for human residents during the summer months. Summer houses ("camps") were constructed here long before any federal or state endangered species legislation was enacted, and long before any evidence of statewide depletion of the snakes was obtained. The private properties are surrounded by state-owned Forest Preserve lands. In this area, humans have lived or vacationed in rattlesnake country for a long time; active field research on *C. horridus* has been carried out for the past ten years (Brown, 1987). Here, most of the landowners now are reasonably tolerant of the snake on their properties and will cooperate with an investigator by calling persons authorized to catch and hold live rattlesnakes (see Removal of Nuisance Rattlesnakes below).

Bounty Hunting and Commercial Collecting

A number of snake hunters over the years have been involved in taking the Timber Rattlesnake for economic gain. The species has, historically, attracted many persons who learned to take it for profit. Hunting the Timber Rattlesnake for monetary gain falls under two categories:

1. *Bounty hunting.*—A number of local governments (usually counties) in several states until recently paid bounties on Timber Rattlesnakes. Such bounties have been paid in Minnesota, New York, Pennsylvania, Vermont, and Wisconsin. They are now outlawed or discontinued in these states.

Effects of the bounty system in causing population depletion are well illustrated in New York and Minnesota. In northeastern New York a bounty was paid continuously for many decades in two counties where rattlesnakes occur. Among a small number of bounty hunters in this region, only two were known to be regularly successful for many years of the mid-20th century. In the last decade of the bounty (1960s) thousands of Timber Rattlesnakes were taken by only one bounty hunter (W. S. Brown, unpubl. data). The same pattern—thousands of rattlesnakes taken by one individual—occurred in southeastern Minnesota (J. Moriarty, 1988 pers. comm.; Keyler and Oldfield, 1992b).

Bounty payments promoted the skills necessary to find and successfully remove rattlesnakes by only a few dedicated woodsmen who dominated the bounty system. They virtually made a living from exploiting the resource at public expense. Like gold prospectors, bounty hunters kept their hunting techniques and localities hidden from others so as to continue their control of the take. Not many individuals got into the act in a full-time way. In both southeastern Minnesota and northeastern New York, the bounty system caused a high level of deleterious exploitation and significant reduction of populations by a mere handful of people.

Extermination is a documentable reality to the present day. In northeastern New York, for example, three distinct den populations (approximately 15% of the known total) were eliminated as late as the mid-20th century by overhunting encouraged by bounty payments (W. S. Brown, unpubl. data). Extirpation of one of these populations is described in an historical account by Stiles (1978): "*In the early years* [1880s], *rattlesnakes were very numerous on the estate... One den..., on what was known as The Cobble, had great numbers of these snakes. For years, Bill Smith hunted the snakes. If anyone wanted a live rattler, he would capture it for him, or if one wanted a skin to make a belt or purse, he would procure that also. The rattles were turned in to the county for the bounty. His son...and grandsons...all but wiped out these poisonous reptiles.*"

Fortunately and paradoxically, in New York bounty hunting did not lead to widespread rattlesnake hunting among the general population. Snake hunting never caught on to become a major outdoor activity promoted by sportsmen's and civic groups as it has in some other states (e.g., Pennsylvania, see SPORT HUNTING AND ORGANIZED ROUND-UPS below).

2. *Commercial collecting.*—This factor is an insidious ever-present current threat, despite some decline in recent years. Stechert (1980) states: "*Over a*

30-year period one person has taken and sold to various institutions over 4,000 Timber Rattlesnakes." This impressive commercial take occurred between the early 1950s through the early 1980s in New Jersey, New York, and Massachusetts. Stechert (1981) says: *"In New York State the overall Timber Rattlesnake population has suffered a 60% reduction since 1900...*[and, referring to the same hominid malefactor]*...no other single individual has had as dramatic an impact on New York State's stocks of* C. horridus." This collector is known today (as of late 1992) to be continuing his illicit depredations. Recently, he was apprehended by Environmental Conservation officers, convicted, and sentenced in New York for illegal taking and possession of Timber Rattlesnakes. This poacher will encounter increasing difficulty satisfying his snake-hunting habits because rangers, wildlife officers, and citizens are increasing their vigilance.

Markets for live Timber Rattlesnakes were traditionally found in roadside reptile "farms" and tourist exhibits. Fortunately, these markets now are decreasing. Today, an increasing market for captured live reptiles is provided by the individual pet fancier. There is a growing number of persons who maintain a surprisingly broad array of reptiles in private collections. Personal collections in the United States and in Europe often contain venomous species. Timber Rattlesnakes, because of their striking coloration and beauty, and their readiness to adapt well to captivity, are much sought-after. One Florida dealer's retail price list in 1991 shows *C. h. horridus* selling for $40 per snake, and another lists 15 specimens available for $45 each.

With resource economics generally, sellers must supply buyers. Private collectors are supplied by market hunters and commercial dealers in an illicit network if the snakes are taken from states in which they are legally protected (see STATE LAWS below). As was the case with bounty hunting, commercial collecting can be devastating to Timber Rattlesnake populations—and it should be stressed that the task can be accomplished by a single motivated individual.

SPORT HUNTING AND ORGANIZED ROUND-UPS

Snake hunting for "sport" is exemplified well by the case of Pennsylvania. In this state the Timber Rattlesnake may be taken legally by licensed individual sportsmen and by participants in organized, privately-sponsored snake hunts in rural communities. Contrary to claims made by hunt organizers, Timber Rattlesnake hunts in Pennsylvania have very little redeeming value for public education. The hunts are acknowledged to be fund-raising events. Although they may raise money for a local organization, their effect on Timber Rattlesnake populations has been harmful. They do nothing except

contribute to the further population decline and habitat disturbance of one of Pennsylvania's irreplaceable wildlife resources. Yet, organized snake hunts in Pennsylvania continue.

Perspectives on rattlesnake "round-ups" in other states, and on other species (mainly *Crotalus atrox*), are in the papers of Campbell et al. (1989), Pisani and Fitch (1992), Warwick et al. (1991), and Weir (1992). These papers are useful for comparison to the information presented here, but are not further discussed.

Recently, two careful surveys and analyses of the effects of organized rattlesnake hunts and the exploitation of *Crotalus horridus* in Pennsylvania have been done. Their conclusions are:

1. *"Organized snake hunts have limited value as a resource management tool, impact negatively upon the resource under consideration* [Crotalus horridus], *and encourage commercial exploitation of wildlife."* (Reinert, 1990).
2. *"We are united in wanting to see rattlesnakes fully protected in Pennsylvania."* (Martin et al., 1990).

Both Reinert's study and the Martin report point directly to a lamentable situation in this state. I see absolutely no good reason to continue to allow a hunt of the Timber Rattlesnake in Pennsylvania. Data in Martin et al. (1990) make a strong case, in my opinion, for complete protection with a full state-wide ban on taking this species.

Pennsylvania provides an excellent case study of mismanagement. Rattlesnake hunting has been shown to cause injury and cruelty to captured snakes, displacement from familiar range, and removal of gravid females from already-depleted populations (Galligan and Dunson, 1979; Reinert, 1988, 1990). This state provides a classic case where hunting an unpopular species for "sport" developed as an annual ritual, or almost a civic hobby, in a number of remote counties (cf. Galligan and Dunson, 1979). Later, the state attempted to gain some control over the resource by licensing hunting as a management tool as might be done with any game species. But, as applied to a reptile species with low biological recovery potential, the "take" has exceeded sustainable levels and the management strategy apparently has not succeeded.

To be fair to the Pennsylvania Fish Commission and to present a balanced view of the controversy, C. J. McCoy (1991, pers. comm.) points out the following: *"The rattlesnake hunter license was originally designed to provide information to the Fish Commission on (1) the number of law-abiding recreational rattlesnake hunters in the state, (2) the annual catch by these hunters, and (3) areas suffering the greatest hunter impact. The hunter permit*

was never intended to serve as a management tool."

For background, in 1985 the Pennsylvania Fish Commission established several new regulations for licensed rattlesnake hunting. These regulations, and others pertinent to amphibians and reptiles, are:

1. An individual permit is required to hunt the snake legally; an annual application and report must be submitted by each license-holding rattlesnake hunter;
2. A bag limit of two snakes per day or two in possession was set;
3. Organized reptile hunt sponsors must apply for and receive a permit to conduct the hunt (the hunt permit recommends, but does not require, that snakes taken be released after the hunt at the location of capture);
4. Reptiles [i.e., rattlesnakes] may not be taken by using chemicals, smoke, explosives, winches, auto jacks, or other device or material that may damage or destroy the den or its immediate surroundings;
5. It is illegal to sell, purchase, import, or export a native amphibian or reptile in Pennsylvania.

Despite these regulations, Martin et al. (1990) indicate that the species is in trouble in the state. This has occurred because the Timber Rattlesnake is being "harvested" in Pennsylvania at a non-sustainable level. The Martin report contains more survey-based field data than heretofore have been gathered on the Timber Rattlesnake in one place over a long time. The report forms an extremely valuable source of information for making wise management decisions.

The Martin report's major findings are:

1. Fully 75% of the rattlesnake dens in Pennsylvania are below levels considered viable (fewer than 45 total snakes or fewer than 8–10 mature females per den; see POPULATION TRENDS and DEMOGRAPHY above).
2. Most of the populations are being decimated by snake hunting.
3. The main cause of the collapse of this resource is the high exploitation of reproductive females during the summer months (see TRANSIENT HABITAT above).
4. Poaching is rampant—most snake hunters report they know of many others who are not licensed and who are taking snakes illegally.
5. The licensing and reporting procedures are a failure. These procedures may even be contributing to the destruction of the snake. The procedures are deficient largely because:

(1) Reporting requirements are not met and are not enforced;
(2) Requiring that all snakes taken be measured is senseless—it is

impractical and probably kills many snakes due to stretching-induced spinal injuries;

(3) Releasing the snakes does not in practice occur at the site of capture as recommended.

Snake hunting is an ostentatious activity: rewards come from removing and "showing off" the catch. Even if released later, as recommended under current regulations, nearly all captured snakes probably will die anyway because of their unfamiliarity with, and disorientation in, a foreign site. I found this statement telling: *"A commonly voiced opinion of snake hunters is that if they turn a snake loose, the next hunter is just going to take the snake"* (Martin et al., 1990). This, in short, is the essence of Garrett Hardin's (1968) *Tragedy of the Commons*, a classic model of resource depletion and environmental ruin.

The pre-1992 legal take (2 snakes/day/person) was much too high. Populations of this snake cannot stand a "harvest" of this size. Human impacts added to the snake's probable low adult mortality rate will only drive populations closer to extinction because the snake has a late age of first reproduction and a low reproductive rate (see REPRODUCTIVE BIOLOGY above).

Without question, the most troubling fact brought out in the Martin report, and in Smith et al. (1991), is the estimated proportion of 75% of dens considered not viable. This is a shocking decline for any species. Martin et al. (1990) state: *"What we find disturbing is not the total estimated number of rattlesnakes* [in the state as a whole], *but the number of dens at which the population is either extirpated, on the verge of extirpation, or below levels considered viable (75%)."* There is hardly a wildlife biologist anywhere who would not recommend, based on this fact alone, immediate protection of the species.

Proponents of continuing to allow sport hunting of the Timber Rattlesnake in Pennsylvania argue that the snake still exists in considerable numbers at some remote dens, even though Martin et al.'s (1990) den estimates (see POPULATION TRENDS above) are evidence to the contrary. Just because a resource seems "secure" in some areas is no reason to become complacent, even if there still may be evidence for its being secure in a few remote areas. As the population status and degree of security are unknown in remote areas, and as "remote" areas themselves are becoming increasingly rare because of enhanced access, the arguments for continued exploitation are questionable. Back-country road construction has paralleled a proliferation of four-wheel-drive and off-road vehicles. Discovering "new" Timber Rattlesnake dens, a common dream of snake hunters, is a thing of the past.

In response to the findings of the Martin report, the Herpetology Advisory Committee—which makes management recommendations to the Pennsylvania

Fish Commission—at its meeting in November 1990 made several recommendations for revising the current regulations. The proposed changes, considered for adoption by the Pennsylvania Fish Commission late in 1991, are as follows:

1. An open season for hunting Timber Rattlesnakes will be restricted from the third Saturday in June until the second Sunday in July;
2. The catch limit will be reduced from two to one;
3. A possession limit of one Timber Rattlesnake per year will be established.

C. J. McCoy (1990, pers. comm.) made the following hopeful points regarding the new proposed regulations: *"These recommendations, if they become regulations, will protect snakes at the den sites and thus protect the dens, prevent stockpiling of snakes, and we hope discourage sport hunting of rattlesnakes altogether."* The three proposals above, if enacted, would have improved the Timber Rattlesnake's predicament in Pennsylvania by reducing rattlesnake hunting to a four-week season with an annual quota of one snake per hunter per year.

Unfortunately, after a public meeting on 4 November 1991, according to a Pennsylvania Fish Commission commentary, *"sponsors of organized snake hunts objected vociferously to several of the proposed changes in the staff draft."* This public meeting resulted in further changes in the proposed regulations which now are:

1. Establish a season for hunting Timber Rattlesnakes from the second Saturday in June until July 31;
2. Reduce the Timber Rattlesnake daily catch limit from two to one;
3. Establish a possession limit of one Timber Rattlesnake;
4. Prohibit importation of Timber Rattlesnakes for use in sacking contests or other prohibited acts;
5. Allow any holder of a permit to catch and possess two (2) Timber Rattlesnakes per hunt while participating in an organized reptile hunt, provided the snakes are released unharmed to the area from which taken at the conclusion of the event.

In evaluating these amendments to the proposed rules, three points should be stressed:

1. Under the original proposals the primary reason for limiting the season to four weeks in late June through early July was to protect reproductive females which become increasingly vulnerable throughout the summer. Gravid females—the snakes usually taken by snake hunters—are those with

the highest reproductive value in the population, and their loss is felt most critically. The regulations being amended to increase the season length to six weeks will only do more harm to the populations by increasing the time available for exploiting gravid females.

2. A catch limit of one snake per day with a limit of one in possession allows wide latitude for individual abuse over an entire season. Unless the take is limited specifically to one snake per year—if that actually is the intent of the regulations—and unless the disposition of any single snake taken is specified (such as, for example, that it must be released at the capture site immediately after capture), the currently-written regulations on the rate of taking (one per day with removal) are not adequate to protect the snake from destructive over-exploitation.

3. It is apparent that in reacting to the vocal objections of snake hunters and advocates of organized reptile hunts, this issue has been at least partly removed from the realm of sound wildlife conservation practice. Input from persons or groups with a vested interest in exploiting the resource has had a negative influence in the decision-making process.

In my opinion these regulations still do not go far enough. The rattlesnake issue in Pennsylvania has degenerated to the level of a political contest. Complete protection, not a reduced hunting season, and not mere discouragement of snake hunting, is required if the Timber Rattlesnake is to recover in Pennsylvania.

Behavioral Disturbance by Humans

Timber Rattlesnakes are susceptible to being behaviorally disturbed by contact with humans. In transient habitats, the snakes' habitual site-specificity gives each transient area its known rattlesnake "hot spots." These "snake rocks" can be learned by snake hunters through experience. It is important to preserve the integrity of the snakes' habitat by not disturbing such sites (see Avoiding Disturbance below).

Disturbance of a "snake rock" may cause abandonment of the site by disrupting the rock itself. Catching or disturbing rattlesnakes at one of these rocks may upset the snakes' normal patterns of behavior. This may involve a snake's experiencing an unpleasant encounter with a human predator and its associating this negative experience with the rock. The snakes' normal habit of basking on the surface in small aggregations is likely to disappear after a few disturbances. In addition, repeated visits to particular rocks frequented by the snakes, and capturing or frightening the snakes at such rocks, will cause abandonment of their use. I and others (R. Stechert, W. H. Martin, B. L. Oldfield, D. E. Keyler) have observed this apparently learned effect at

numerous places over many years. As pointed out by Brown (1992b), the phenomenon deserves study.

The effect of disturbance by humans is controversial among Timber Rattlesnake biologists. Some researchers feel that this phenomenon is trivial or nonexistent, others that it is real and significant. Quotations supporting each school of thought follow:

Observations Doubting the Importance of Disturbance.—Among those who feel that human activities do not unduly disturb Timber Rattlesnakes are H. K. Reinert and R. T. Zappalorti who have done extensive field studies of free-ranging rattlesnakes using radiotelemetry. These workers have commented as follows:

"After 13 years of radiotracking this species in both Pennsylvania and New Jersey, unlike some other species I've monitored, Timber Rattlesnakes allow themselves to be closely approached while they are engaged in almost any activity. The presence of a non-threatening human observer usually elicits only brief curiosity on the part of the snake and practically never a fright or defense response. Normal activity is resumed shortly after the observer has left the snake's visual field. Likewise, even capture and release or constant approach and observation have little impact upon behavior patterns.

"Human-disturbed areas, such as road edges, gravel pits, clear cuts, and trails are often used by Timber Rattlesnakes as basking or foraging sites. Frequently, foot and automobile traffic passes literally within meters of the snakes without eliciting a fright or defense response and without causing the snakes to abandon the site. Several snakes have purposely used people's backyards and stayed there despite the presence of large dogs and power lawn mowers. Similarly, Timber Rattlesnakes show no aversion to crossing busy sand or gravel roadways (sometimes to their demise)." (H. K. Reinert, 1991, pers. comm.).

"I suggest that rattlesnakes are not as susceptible to humans attempting to catch them or walking through their basking areas as you state. Even if you capture a rattlesnake, take it to the laboratory, brand it, surgically implant a transmitter, measure it in a 'squeeze box,' then release it, the snake will still return to its original capture location. This was the case with at least four of the rattlesnakes we monitored over a 3-year period. They would return to the same stumphole, shelterboard, or log once or twice during their spring, summer and fall activity seasons." (R. T. Zappalorti, 1991, pers. comm.).

Observations Supporting the Importance of Disturbance.—Several field workers who primarily capture and process (measure, mark, and release) Timber Rattlesnakes have noticed an apparently real disturbance effect. In addition to my observations (above), B. L. Oldfield, D. E. Keyler, and R. Stechert comment as follows:

"We feel strongly that field processing Timber Rattlesnakes (i.e., pinning,

restraining, probing, taking body temperatures, palpating, measuring, marking, bagging, and weighing) causes considerable 'psychological stress' to the animal—even when the procedures are accomplished expediently and without unnecessary force. In some way the snake must relate this processing as an encounter with a very large predator that resulted in a survival struggle. After release at the capture site, the snake often leaves the site (escaping the odors of humans, trampled vegetation, and rattlesnake musk) within a day or two. They may not return for an extended period (months or even years.) The Timber Rattlesnake is a secretive wilderness species that relies heavily on avoidance of potential predators as an essential survival technique. Certainly, a field-processing encounter with a human would be something to avoid in the future." (B. L. Oldfield and D. E. Keyler, 1991, pers. comm.).

"I have observed Timber Rattlesnakes that have been exposed to repeated human harassment over a number of years develop a tendency toward reluctance to expose themselves at their primary basking rocks, both around their dens and at adjacent basking areas. This is not unusual behavior in light of the stress they must experience (even if carefully handled) after several recaptures or near-misses. In 23 years of repeated field trips to 24 Timber Rattlesnake den sites and their basking areas, I have noted this phenomenon (which I nickname the 'spook factor') at 15 of the most frequently visited dens. Additionally, when these populations are left alone for five years or more the snakes appear to begin to lose their apparently learned caution and bask more openly." (R. Stechert, 1991, pers. comm.).

Resolving this issue will require more research. At this point it appears that a possible methodological difference is contributing to the divergence of views on behavioral effects on the snakes. If an investigator quietly approaches an individual rattlesnake being radiotracked the effect may be very different from that of an investigator who captures and processes the snake. Physical restraint is probably much more stressful to the animal than is distant observation.

Vegetative Changes

In some regions, several investigators believe that "shading over" on and near a den, or natural successional increase of overstory canopy closure by an increase of the growth of large trees, may be causing conditions that are incompatible with long-term viability for Timber Rattlesnakes. Eventually, such growth of vegetation may make a den unsuitable for occupancy and cause its extinction. There is a need for an open, lightly wooded or brushy early successional plant association to provide an optimal denning environment, according to this view. Again, there is no consensus among several workers. Thus the effects of this threat and how to deal with it are controversial (see

HABITAT ENHANCEMENT below). Few exact data are available; more research is needed.

W. H. Martin (1990, pers. comm.) says: *"Shading-over of the den site does not present a problem for snakes at emergence time when the trees are bare or just starting to leaf. The problem is shading-over of the rocks that are used as gestating and birthing rookeries."*

W. B. Allen (1990, pers. comm.) has made extensive observations on this problem in western Pennsylvania. He says: *"Many of the dens that I hunted twenty or more years ago today are no longer used by the Timber Rattlesnake. It has not been due to collecting by snake hunters. It is mainly due to the forest growth of young trees, including mountain laurel and rhododendron. The trees and brush have grown up in and around the den, shading it over. My theory is that many of the dens have become too shaded-over for the snakes to utilize them and they have moved out. The snakes will not stay in the den site area. In these shaded dens the only places we see the snakes is in a small sunny spot, nowhere else. There is no sunlight or warmth to keep them there."*

In the midwest, along steep cliffs (palisades) of the Mississippi River in northwestern Illinois, B. J. Bielema has conducted surveys of the Timber Rattlesnake. He believes that succession has contributed to the decline of *C. horridus*, reporting as follows: *"The growth of shrubs and trees is believed to be a limiting factor* [which] *may rank with the deleterious effects of over-collecting, direct killing, and destruction of habitat. An early photograph shows outcrop bluffs denuded of trees. Many trees were cut for use in the steamboats of the era. Snake numbers during this time were thriving. Today the palisades are barely visible during the summer due to the heavy forest present."* (Bielema, 1991).

A contrasting vegetative change has been occurring in some areas, that of some forests being opened up by herbivorous insect pests. The effects of these community changes are yet unknown and unstudied. Observations are recorded by S. H. Harwig (1991, pers. comm.): *"In the past few years, there is a new vegetative change in the vicinity of many Pennsylvania dens, due to greatly diminished shading caused by oak leaf roller worms and gypsy moth caterpillars eating 10 to 90% of tree foliage and killing many trees. The increased sun reaching the ground has caused a proliferation of growth of ferns, blueberry, greenbriar, blackberry, and young trees. The underbrush is heavier than it used to be in north-central Pennsylvania, but the growth is more pronounced in some of my southwestern Pennsylvania dens. Fortunately, most of the good upstate rattler country has very little greenbriar or blackberry."*

Mr. Harwig's last comment refers to an area's easier accessibility by humans in walking through wooded habitats compared to the great difficulty of traversing briar- and brush-choked areas. Thus, insect pests and consequent

heavy underbrush, paradoxically, may lead to discouragement of snake hunters from entering such areas and may incidentally help to protect some rattlesnake dens from humans.

Blasting and Filling-in of Dens

These methods probably have been used in an attempt to eliminate Timber Rattlesnake dens far more often and in more places than has been recorded. Two observers have made notes on instances of each type of attempted direct killing effort.

R. Stechert (1991, pers. comm.) records the following: *"On 21 August 1981 I interviewed Mr. Kort Burnham, a lifetime resident of Willsboro, Essex County, New York. During the 1940s Mr. Burnham was hired by the New York State Fish and Wildlife Agency for an experimental eradication program of a Timber Rattlesnake population that occurs on a nearby mountain. To this end he dynamited three separate areas in the primary den rockslide. He believed the blasting had little effect on the local population. Approximately 40 years later, Bill Brown, Marty Martin, Steve Harwig and I visited the site. We found the three blast sites, recognizable by considerable hollows in the face of the rockslide. In spite of Mr. Burnham's blasting, the area appeared to still support a moderate population of* C. horridus."

In northwestern Illinois, Bielema (1990) records the following account of an eradication campaign at a state park: *"The park's history shows the Timber Rattlesnake figuring prominently in the early years of its existence. Much controversy resulted when it was decided to eliminate the rattlesnakes from the park, originally purchased in 1929 with an acquisition of 420 acres.* [The park superintendent] *would not be easily dissuaded from the course of action he decided to take. This was to introduce sheep and hogs into the known den areas as well as fill the den crevices with concrete. Objections arose mostly because of the fear that the sheep and hogs would destroy the wildflowers of the park.* [The park superintendent] *finally authorized the filling of the den crevices with concrete, hiring men to kill the snakes at $1.00 per snake, and introducing hogs in a small enclosure near the main den area. In 1936, several years after the initial action was taken, a letter from the superintendent of state parks stated that few rattlesnakes had been seen in the park over the last two years and that the CCC camps were continuing to fill in the dens with concrete."*

During 1989 and 1990, Bielema (1990) recorded no rattlesnakes in 24 search days totaling 50.2 hours at the park. He concludes his survey by saying *"It is questionable that a viable population now exists there. The eradication method of cementing dens may have been effective...*[and]*...direct killing of the snakes was also a successful eradication technique."*

Logging, Mining, Gas Wells

Commercial tree removal may not necessarily cause long-term harm to a Timber Rattlesnake population's habitat. The key term here is "long-term," for considerable short-term damage to the snake's summer habitat can occur by logging activities. Studies by Reinert (1984a, b) and Reinert and Zappalorti (1988a) have documented the heavy canopy cover preferred in deeply shaded woods by Timber Rattlesnakes on their summer range. Such canopy closure would be opened by logging, negatively impacting the snake's preferred habitat. Wherever possible, logging should be restricted or prohibited within the snake's primary summer range area (see Land Protection below). Also, as logging can pose a direct threat to the snakes if conducted during the summer months, it should be restricted to the winter season if it occurs within rattlesnake range.

Mining or rock quarrying threatens some populations. In New York, A. R. Breisch (1991, pers. comm.) says: *"Several of our old dens are near quarries, and in a recent case the mining company withdrew its plans, in part, because of an associated Timber Rattlesnake den."*

Gas wells increasingly are encroaching upon Timber Rattlesnake habitats in some areas. In Pennsylvania, S. H. Harwig (1990, pers. comm.) observed: *"May 23: We went to a good den where I saw a pile of 12–20 rattlers on August 17, 1989; the area now has gas wells which may encroach on the den. June 10: At the 'far end' of one of the most remote areas* [of a long-studied denning area observed by Mr. Harwig for many years], *I was shocked to see a recently-made clearing and a tank signifying a gas well site."*

LAND PROTECTION

If it were not for the existence of public lands (e.g., national and state parks, state forest preserves) and of privately owned nature preserves, much of the remaining habitat of the Timber Rattlesnake already would have been destroyed. Rattlesnakes on private properties, increasingly being developed, are vulnerable. Thus, taking steps to increase public land holdings in prime remaining Timber Rattlesnake habitats through a variety of purchase or conservation easement mechanisms is an important conservation strategy for this species.

An adequate area of undisturbed summer range habitat surrounding a Timber Rattlesnake den is vitally important for protecting a viable population. A. R. Breisch, Senior Wildlife Biologist of New York State's Endangered Species Unit (1991, pers. comm.) suggests defining a den site's quality by whether disturbance is too close. Mr. Breisch says *"Long-term integrity of a den can't be assured if only a few hundred acres are protected."* As yet, no

formal proposals for defining den site quality based on degree of disturbance at various distances have been attempted. Such an effort should be a conservation objective of high priority.

The distances from known dens on which protection of the snakes and their habitat is based will need careful determination. As noted above (see SPATIAL BIOLOGY), occasional individual rattlesnakes are known to move as far as 4.5 miles from their den. The maximum migratory distance averages 2.5 miles for males. With the den as a central focal point, a radial distance of 2.5 miles in all directions from a den yields a total area of 19.6 square miles (51 km^2) of habitat area for a healthy population.

In many areas it may be impossible to obtain an unbroken circular tract of land of this extent around a den, and it also may not be biologically realistic in terms of the snakes' movement patterns. Some populations apparently use "corridors" for their migrations in certain directions, thus making some segments of habitat far more heavily used than others. Timber Rattlesnakes seem to avoid difficult sheer ledges that may rim one side of a den, and, where dens are at a lower elevation than is summer range, most of the snakes tend to go upslope to areas of higher elevation.

Home range size has been reported to average about 160 to 500 acres for males and about 40 to 100 acres for nongravid females (Reinert and Zappalorti, 1988a; Reinert, 1991b). Considering that home ranges may be often non-overlapping, or may occur in separate areas of the available habitat, it would be prudent to expect the total area used by a healthy Timber Rattlesnake population of about 50 adults to occupy at least 7 square miles. This requires 1.5 miles of protected land in all directions from the den. A distance of 1.5 miles radius from a den (total area = 7 square miles or 18 km^2) will protect most females and many of the males.

In addition to the recommended 1.5 mile radius for adequate protection of habitat for a population, a buffer zone of 1.0 mile beyond this is recommended. This buffer zone might be habitat of lesser quality or it might contain some human incursion. This additional area, even if it consists of moderately disturbed habitat, will accommodate those rattlesnakes that move up to 2.5 miles from their den (an approximate average maximum distance of migration for males and for some nongravid females) and will offer additional protection to the population.

Although a 2.5-mile migratory distance as a measure of radial protection from a den applies to many populations, in some areas and at some dens this distance still may be less than the maximum distances moved by some snakes in the population. Each specific area should be studied in detail to ascertain the patterns of movements of migrating rattlesnakes. In general, as a working recommendation, an area within 1.5 miles of a den seems critical for protecting Timber Rattlesnakes in most denning populations studied to date.

RECOVERY POTENTIAL

There have been no studies of population dynamics, and no quantitative data to document actual recovery potential. Most workers with good knowledge of the species believe depleted populations of *Crotalus horridus* can recover. Martin (1990, pers. comm.) reports the following: *"One den that had been depressed to about 50 to 60 snakes in 1968 by hunting pressure had climbed to about 120 to 130 snakes in 1983* [a 15-yr interval]."

The exact minimum viable population size and timing of recovery are unknown. What follows is speculative, but based on sound biological intuition. Minimum population size needed for recovery probably must consist of approximately 30 to 40 snakes with an even age distribution, with at least four or five mature females. Given the late age of maturity and slow rate of reproduction (see REPRODUCTIVE BIOLOGY above), recovery probably would require many years. If such a small population were completely protected, it might gradually build up to an average den size of 60 to 100 animals with a representative age distribution within twenty to thirty years.

BIOLOGICAL MONITORING PROCEDURES

There is a need for the most basic records to be kept in a uniform way at particular dens over extended time periods. Long-term quantitative observations would help to fill an important monitoring void. Monitoring is necessary to show population trends over long time scales necessary in long-lived species such as *Crotalus horridus*.

The most uniform procedures recommended for comparable monitoring between areas are:

1. *Sighting Rate.*—A sighting rate most effective for comparisons is *snakes seen per hour.* This is achieved by walking or searching prime habitat and counting all rattlesnakes identified as such (i.e., whether actually seen or not). That is, a snake that gives itself away by rattling under rocks, or that is glimpsed while escaping, should be counted.

2. *Capture Index.*—A capture index is effective when snakes are actually caught in mark-recapture population studies. Trends may be shown over seasons, and between months, by calculating the number of snakes caught per capture day or per field day. A *capture day* is defined simply as any day on which at least one rattlesnake is caught and a *field day* is a sampling day on which concerted searching takes place (Brown, 1992b).

Each of these methods may be refined by including sightings only on days when at least one rattlesnake was seen (a *sighting day*), and may include the

number of observers involved if sampling by several persons occurs at the same time and place. Thus, an index of *snakes seen/sighting day*, *snakes seen/field day*, or, in combination with total time spent in the field, an index of *snakes seen/hr/person* may be feasible.

BIOLOGICAL MONITORING PROGRAMS

Active monitoring/research programs on Timber Rattlesnake populations are being conducted in the following states by a number of individual researchers. An alphabetical list of these individuals, with their addresses and telephone numbers, may be obtained from the author on request. These individuals and their state(s) are:

Arkansas—S. E. Trauth
Connecticut—D. F. Fraser, R. W. Fritsch II, M. W. Klemens, R. C. Petersen.
Iowa—J. L. Christiansen, B. J. Bielema.
Illinois—B. J. Bielema, D. Storment.
Indiana—S. A. Minton Jr.
Kansas—J. T. Collins, H. S. Fitch, G. R. Pisani.
Massachusetts—T. F. Tyning, T. W. French, T. Palmer.
Maryland, *North Carolina*, *West Virginia*—W. H. Martin.
Minnesota, *Wisconsin*—D. E. Keyler, B. L. Oldfield.
Missouri—W. J. Drda, T. R. Johnson, O. J. Sexton.
Nebraska—J. Lokke, J. D. Lynch.
New Hampshire—J. T. Taylor, A. Soha.
New Jersey—R. Stechert, R. T. Zappalorti.
New York—A. R. Breisch, W. S. Brown, A. Peterson, A. C. Smith Jr., R. Stechert.
Ohio—D. Wynn, M. Hall, G. T. McDuffie, S. Moody.
Pennsylvania—W. A. Dunson, S. H. Harwig, W. H. Martin, C. J. McCoy, H. K. Reinert, W. H. Smith, R. Stechert.
Virginia—W. H. Martin, J. C. Mitchell, A. H. Savitzky, B. A. Savitzky.
Vermont—M. DesMeules, C. W. Kilpatrick.

RESEARCH NEEDS

Research is needed on the following specific biological questions (listed in order of priority of conservation needs) concerning *Crotalus horridus*:

1. Long-term comparative measures of population trends; quantitative data on population densities;

2. Mark-recapture estimates of population sizes of denning colonies including tests of assumptions of random sampling;

3. Age-specific survivorship, particularly among newborn and snakes in the first year;

4. Factors causing mortality: assessment of role of density-dependent and density-independent factors;

5. Reproductive biology of females: age of first reproduction, reproductive frequency, litter size;

6. Detailed seasonal movements of adults in communally denning populations;

7. Mechanisms of den-finding in newborn; movement patterns of newborn from birth site to den;

8. Ability of translocated, repatriated, or introduced rattlesnakes to "take to" and become established in a historical site or formerly extirpated den.

RESEARCH PROGRAMS

There are several research programs underway. The following states and researchers (see BIOLOGICAL MONITORING PROGRAMS above) are conducting research on the questions as listed in RESEARCH NEEDS above:

Connecticut—Fraser and Fritsch (1, 2, 3, 4, 5, 6)
Kansas—Fitch and Pisani (6)
Minnesota—Oldfield and Keyler (1, 3, 4, 5)
New York—Brown (1, 2, 3, 4, 5, 6); Stechert (1, 4, 5, 6); Smith (1)
Pennsylvania—Reinert (6, 7, 8); Harwig (1)
Virginia—Martin (1, 2, 3, 4, 5, 6)

A number of the primary contact persons are actively studying other aspects of the Timber Rattlesnake in their areas, usually watching its general status, mapping its local distribution, and working in educational or regulatory efforts to protect it. The above list of studies more specifically includes those individuals working on research questions of significance for understanding the basic biology of this species with direct reference to its ecological management and long-term protection.

An important regional meeting recently brought together many biologists and conservationists interested in protecting and managing *Crotalus horridus*. The meeting, "*Conservation of the Timber Rattlesnake in the Northeast*," was held on 7 December 1991; symposium notes from the meeting, containing state status reports and conservation and life history surveys (T. F. Tyning, Ed., 1992), may be purchased from the meeting's sponsoring organization,

the Massachusetts Audubon Society, South Great Road, Lincoln, Massachusetts 01773.

MANAGEMENT PROCEDURES

The Timber Rattlesnake can benefit from active management. Specific management strategies recommended are:

Protection

The Timber Rattlesnake must be actively protected against taking and killing by humans. This may involve patrolling and/or guarding an area against commercial reptile collectors and general poachers.

Fencing

A related (but contrary) approach involves protecting humans against rattlesnakes. A barrier technique such as fencing can, in certain situations, result in protection of the snakes. For example, at two adjoining vacation camps in New York, the landowners cooperatively erected a hardware cloth "snake fence" around their camps (even though the materials were somewhat costly, and the fencing was labor-intensive). The snake fence was modeled after those erected around snake dens in Utah by Parker and Brown (1973). It was built of steel posts (concrete reinforcing-rods, or "re-bar") spaced approximately 2 m apart, and with half-inch (1 cm) galvanized hardware cloth wired in place. The fence was buried into a shallow trench and covered along its base with soil, stones, and leaves. Height of the fence was approximately 3 feet (1 meter) and its total length was about 250 m.

Erected in the early summer of 1986 and in place now for seven years, the fence provides a snake-proof perimeter barrier against encroachment by rattlesnakes. Not one Timber Rattlesnake has been seen by the landowners near their camps. In contrast, for several decades prior to its emplacement, usually during July and August at the height of the mating season, several rattlesnakes had been seen (and most killed) regularly each year. The success of this fencing procedure in deterring rattlesnakes from moving onto private property has been an important factor in increasing the peace of mind and cooperation of these landowners (see Education below).

Maintenance of Secrecy

It is essential to never reveal the location of hibernating dens to anyone, except for valid reasons (e.g., research or protection). Local media and

popular magazine writers, in particular, should not be given specific locality information. Care should be taken in this regard also in dealing with land developers. It is advisable to know the motives of seemingly innocent but inquisitive individuals who say they just want to "see" or "photograph" a Timber Rattlesnake.

More than all other factors, it is this lapse of judgment on the part of those with this sensitive knowledge which has, over the years, led to massive exploitation. Prime examples are the early popular writings of Kauffeld and of Ditmars which gave away specific localities. The sites they mentioned were subsequently visited by many snake collectors, and, in most cases, these localities were decimated.

A series of letters was published in *Herpetological Review* in 1984 debating the issue of balancing the need to take specimens of rattlesnakes for scientific investigations against the need for conservation. In one letter (Herpetol. Rev. 15:100–101), referring to dens of the western rattlesnake, *Crotalus viridis*, I pointed out one prime example of this problem: *"The impact of identifying the locations of the dens may well be the most serious problem for these denning colonies in the long run. Exact locations (distances and directions from towns, elevations), as well as publication of the local names of the dens, may ensure that these denning colonies will receive increased attention from snake hunters and unscrupulous collectors."*

Herpetologists also have debated the effect of removing female western rattlesnakes from denning populations for the purpose of studying their reproductive biology. In the same letter (op. cit.) I said: *"Forty years ago in Utah, the well-known Woodbury den contained around five hundred Great Basin rattlesnakes* [C. viridis] *but within twenty-five years the population had been reduced to a mere remnant of about two dozen snakes largely because the location of this den was revealed to numerous persons in the belief that such knowledge would promote conservation through education. After the word spread, however, it did not take long for human predation to virtually extinguish this once-spectacular aggregation."*

Secrecy is relative, however, and, although sensitive, sightings of the Timber Rattlesnake can be exchanged among biologists and managers. Dissemination of known occurrences can greatly help evaluate regional status. L. L. Master, Chief Zoologist with The Nature Conservancy (TNC), points out an important aspect of this (1991, pers. comm.): *"Perhaps the most useful thing that biologists and other rattlesnake observers can do to assist in conserving Timber Rattlesnakes in states where rattlesnakes are rare is to ensure that all field observations are relayed to the State Natural Heritage Program. A comprehensive listing of the 50 state and other (e.g., provincial) programs is maintained by TNC. These databases are staffed by persons sensitive to the secrecy requirements of rattlesnakes and other rare collectable*

species. The protection agenda of TNC and some state agencies are derived from these State Natural Heritage Program databases. They also help protect snakes through their use in a state's environmental review process."

Avoiding Disturbance

Timber Rattlesnakes on their dens and in transient habitats are likely to be disturbed. Thus, visits to den sites and to specific shelter rocks in transient habitats should be curtailed to avoid agitating the snakes. Disturbance can occur not only by snake hunters, but by casual visitors and otherwise well-meaning observers. Repeated visits to den sites or to specific "snake rocks" can put the normal behaviors of these snakes at risk of disruption.

As noted above (see Behavioral Disturbance by Humans), however, some researchers point out that Timber Rattlesnakes may tolerate humans in situations where the snakes are not caught and handled, but rather are observed from a distance. For example, using binoculars, such observing has been carried out successfully by A. C. Smith Jr. in New York where individual rattlesnakes are monitored frequently. But also, some observers frankly object to restrictions on field visits as recommended here. Tom Palmer (pers. comm., 1991) makes this case: *"These suggestions, I must admit, make me nervous. If implemented, they would cancel my seasonal pilgrimages to see rattlesnakes. My credentials are dubious; I have no 'need' to see the snakes. And yet, since I found them myself (after several years' effort), and visit them regularly, I take a proprietary attitude—I feel I have as much right to be there as anyone else, and don't worry particularly about whether I might be upsetting them (they seem to take no notice of me)."*

Patrols during Vulnerable Times

There are two periods when Timber Rattlesnakes are especially vulnerable: (1) During *spring emergence* (late April to mid-May in the north), and (2) during *gestation and birthing* (early July to late September in all areas). Both times of susceptibility to human predation occur when the snakes are located on or near their hibernating dens. During these times closing off access to the den itself is an important action. Also, the researcher/manager may want to simply avoid disturbing the animals during these vulnerable periods unless these periods are being used to conduct specific counts for population estimates (see Determination of Occurrence above).

Habitat Enhancement

The factor of shading-over is summarized under Vegetative Changes, above. The threat itself, and what, if anything, to do about it, are somewhat

controversial among Timber Rattlesnake biologists. W. B. Allen (1990, pers. comm.) suggests an active management approach to the problem of shading-over: *"A very easy solution to the problem is for the various branches of state government—game and fish, land management, state forest service and their maintenance personnel—to go into these shaded-in areas during the winter months and cut some of the brush that is shading the den sites. It would not be a massive project. Most of the dens observed have small trees growing up from the base of the den where the soil is. As they reach the area just above the rocky ledges, the sun causes the foliage to thicken thus shading the rocks beneath them. All that has to be done is for the timber crew to drop these trees downhill below the den. They do not need any equipment except for their saws. The brush can all be dropped at the base of the ledges and left there. This project, when done in winter, will not harm the snakes nor will the crew encounter any rattlesnakes which would possibly pose a threat to them while timbering."*

Zappalorti and Johnson (1981) have advanced a management plan for some Timber Rattlesnake populations in New Jersey, although they state that as of 1 January 1988, the proposed plan had not been implemented. They state: *"Management of northern populations would consist of cutting back trees that have overgrown and shaded the rocky den area. When the canopy becomes too thick, it prevents sunlight from reaching the rocks where the snakes bask."*

Several areas in the midwest seem to have changed in recent decades by vegetative overgrowth of formerly open rattlesnake habitats. If these areas are to be enhanced for rattlesnake habitat, they may require active tree removal. B. J. Bielema has conducted surveys in state parks in northwestern Illinois and (1991, pers. comm.) writes: *"Former residents of the nearby nature preserve detailed many den localities within the preserve property before dedication as a preserve. The forest now has covered over most of these. The complete canopy of the parks allows no open talus or bluff to exist. The den area is showing signs of the spread of the forest and will need to be thinned. The rampant spread of red cedar as well as broadleaf species across the bluff face, over the talus below, and hill prairie above, needs to be controlled. Perhaps fire and a dry climate enabled these open areas to persist in years past. Fire may still be a tool to consider in some circumstances."*

One worker (A. C. Smith Jr., 1991, pers. comm.) has actively managed one den area by selective felling of larger shade trees (vegetation thinning) in the vicinity of a den on a Nature Conservancy preserve in southwestern New York. Dr. Smith also has actively intervened to enhance basking areas near a den by increasing available shelter rocks. He says: *"In addition to vegetation thinning, I also enhance or create new stone piles. Some new piles become occupied the same year of construction and other piles that have been by-*

passed for years now become regular basking areas. Once a stone pile gets covered with sticks and leaves it is not generally used."

Whether tree removal and other clearing operations may be a strategy useful to enhancing denning habitat is, however, questioned by H. K. Reinert (1991, pers. comm.): *"Dens are never shaded over at spring emergence or fall ingress because there are no (or few) leaves on the trees at these times. It also appears that many dens in Pennsylvania are historically situated in sheltered, heavily wooded areas. Removal of trees from such sites may actually do more harm to the den by decreasing fall leaf litter cover (a good insulation in low-snow winters) and exposing the surface to harsh winds and temperature extremes that the woodlands tend to buffer. Tree removal may also alter ground water levels, something that I feel may be critical to winter survival. In all likelihood, the lack of adequate open summer basking sites for gravid females may be more detrimental to populations than shading over of hibernacula."*

R. Stechert (1991, pers. comm.) has a different view from that of Reinert on fall shading at dens, and, like Allen, Zappalorti, Bielema, and Smith, advocates tree removal: *"Except for the most exposed rockslides, dens are always partially or completely shaded over during fall ingress. I have several times seen crevice dens that were becoming so clogged with leaf litter that the rattlesnakes made burrow holes in the debris to reach their hibernating crevices. With the common practice of fire suppression by forest agencies, this is not surprising. Removal of a few trees in the den area helps prevent debris accumulation and offers a better exposure at heavily shaded sites immediately prior to fall ingress. The detrimental aspects of the shading-over of den crevices and adjacent basking areas have been seen at several locations, particularly by me in Schoharie County, New York, and Allegany State Park, New York, and by Steve Harwig in Allegheny National Forest, Pennsylvania."*

Not always is there a problem with the habitat undergoing succession. Agents such as insect pests can reduce overstory cover by defoliation, and may impact Timber Rattlesnake habitats by making them more open, but with as yet unstudied and unspecified effects on the snakes (see VEGETATIVE CHANGES above). Solving the problem of vegetative changes in the snake's habitat, including shading-over and defoliation, will require much more analysis. There seems to be an abundance of long years of observational evidence by several competent observers that the shading-over effect is real. Managing a shaded-over area by vegetation thinning can most fruitfully be recommended once data show clearly a decline in the snake's density owing to shading-over and not to some other factor, such as human taking, that happened simultaneously. As in many areas of ecology where long-term quantitative data are required, no hard evidence is available from annual samples of vegetation density and correlated snake censuses.

Restriction of Logging

In the vicinity of a den, logging should be conducted only during the winter months of November through March (five months) and avoided during the snakes' active season, April through October (seven months). This will prevent the snakes from being killed by loggers. More fundamentally, whether to undertake extensive tree removal within the primary summer range of *C. horridus* should be examined carefully as logging reduces canopy closure, thus altering an important factor in the snake's environment (see Logging, Mining, Gas Wells above). Logging should be restricted or prohibited within the summer habitat of a viable population.

Translocation

Many historic locations exist throughout the Timber Rattlesnake's range where the snake has been extirpated (see Population Trends above). Some den sites may be good candidates for *repatriation*, or intentional release of individuals of a species into areas formerly occupied by that species (Reinert, 1991a). To my knowledge, there have been no soundly-based attempts to repatriate *Crotalus horridus*. Under the definition of *augmentation* (Reinert, 1991a) as *"the specific type of translocation that involves the release of individuals of a species into an area already occupied by that species,"* efforts to augment existing populations of the Timber Rattlesnake also may be feasible.

There may well be utility in restoring viable populations of this species through translocation, if done judiciously. A word of caution is in order, however. An ample review of the various translocation techniques by Dodd and Seigel (1991) showed that among amphibians and reptiles only 19% of translocations were successful. In proposing to re-establish *C. horridus* at any of its historic localities, I would advocate fully justifying the proposed project and adhering to the biological guidelines for monitoring the success of the project as recommended by Dodd and Seigel (1991).

Education

Educating people about venomous snakes indeed poses a major challenge, but it is not impossible. Leaflets, signs, and public lectures are all important aspects of a campaign of biological knowledge that can have a positive effect in conserving and managing these animals. Reinert (1985) says: *"The realization that rattlesnakes are an integral part of the deciduous forest ecosystem has not received widespread public acceptance. Consequently, most rattlesnakes are indiscriminately killed even when encountered miles*

from populous areas or human habitations. Educational programs designed to dispel prevalent myths concerning rattlesnakes and to foster an understanding of the importance of the rattlesnake in the ecosystem should be developed and made available to schools, sportsmen groups, park naturalists, and other outdoor-oriented organizations."

More and more, as people become exposed to accurate information about wildlife and natural communities, fewer and fewer nongame species will be taken or slaughtered. A good example of general natural history writing that includes a biologically accurate description of *Crotalus horridus* in its natural habitat is provided by Kricher and Morrison (1988) who write: *"Snakes represent excellent examples of cryptically colored animals. Many species blend quite closely with the background pattern of their habitats. Both the Timber Rattlesnake and the Copperhead are members of the highly poisonous pit viper family and both are extremely well-camouflaged dwellers of the shady forest floor."*

Removal of Nuisance Rattlesnakes

In two Timber Rattlesnake study locations where active research is being carried out (Connecticut by Fraser and Fritsch, New York by Brown), printed information for residents is distributed. The material for nuisance problems in northeastern New York says that occasionally a Timber Rattlesnake may present a "nuisance" by being found near buildings, roads, or campsites where it may pose a threat to human safety. Persons are advised to stay away from a rattlesnake and to call a trained wildlife biologist, state Environmental Conservation Officer, or state Forest Ranger who will remove the snake. Names and telephone numbers are provided. In Connecticut, the state Department of Environmental Protection now sends a two-page letter concerning rattlesnakes to landowners which states, in part: *"Since some of the folks receiving this letter will be new to the area, we need to advise that the Timber Rattlesnake is a protected species in this state. We also need to advise that the average person should not attempt to capture a rattlesnake. Please report any dead rattlesnakes, because important information can still be obtained* [from a dead specimen]" (P. L. Good, Supervisor of Wildlife Research, Connecticut D. E. P., 1990).

Important keys to achieving cooperation from landowners is their knowing the rattlesnakes are part of a biological field study, and that there will be a rapid response to remove a nuisance snake. At the New York study site, and increasingly at the Connecticut site, many residents are strongly inclined to cooperate and to take part in the removal and protection programs. This knowledge and active involvement by local residents, and personal attention

to them by the researcher or manager, are important factors in successfully protecting Timber Rattlesnakes.

Signs

On some lands where the Timber Rattlesnake occurs, whether public or private, informational or warning signs may help to inform visitors or hikers of the presence of the snake and may enhance educational efforts for protecting it. The signs may, on the other hand, be viewed negatively by managers and researchers in that they do advertise the snake's presence to collectors or poachers. Composing a good sign is fraught with difficulties, namely the dilemma of offering too little or too much information of particular types. Whether to incorporate signs will depend on one's judgment of the situation, as discussed above (see Maintenance of Secrecy). Three examples of signs follow:

> *TIMBER RATTLESNAKES* live in this park but are not numerous. Being timid, they offer little or no threat to park visitors. If you are one of the few people to see a Timber Rattlesnake, leave it alone. Do not try to capture or kill it. Like all park wildlife, they are protected. If you have a camera along, you might wish to take a photograph. Please report sightings to the park office.

(Minnesota Department of Natural Resources sign for state parks, courtesy Barney L. Oldfield.)

> *NOTICE*—Specimens of the Timber Rattlesnake have been found along this trail in limited numbers. This snake almost invariably warns of its presence by sounding the rattle. The use of leather boots or high shoes (not oxfords) and care in the use of hands in climbing are recommended as precautionary measures.

(New York State Department of Environmental Conservation trail sign, in part; a final section on treatment of snakebite is lengthy and outdated, and is omitted.)

For replacement of the trail sign in use (above), in 1979 I suggested a different sign for state lands in New York. For the general reasons stated above, however, implementing it was not further pursued. Due to the recent snakebite first aid measures recommended by Hardy (1992), an updated version of this proposed sign reads:

RATTLESNAKES are found in this area. Watch where you step. A rattlesnake will not attack, but it will strike if stepped on. Do not approach or molest a rattlesnake. If you see a rattlesnake, stay away from it. The Timber Rattlesnake is a threatened species and is fully protected by New York State law. It is illegal to take, import, possess, transport, or sell a Timber Rattlesnake in New York. IF BITTEN:

1. Stay calm: A rattlesnake bite is serious but is rarely fatal.
2. Restrict movement of the bitten limb; if possible, splint it and keep it below heart level.
3. Walk slowly out of the woods.
4. Go to the nearest hospital immediately.

MANAGEMENT PROGRAMS

State Laws

A state-by-state abstract of wildlife regulations affecting *Crotalus horridus* has been written recently by Breisch (1992). The following summary relies mainly on Breisch's tabulation but should be taken to be in flux as wildlife statutes in the various states are often undergoing revision. Thus, no listing of state regulations in broad categories is likely to be completely settled at a given time of writing.

Among thirty-two U. S. states and one Canadian province (Ontario: listed as endangered, but probably extirpated) of extant or former occurrence, thirteen states provide some measure of legal control of taking or selling, or partial protection of all herpetofauna or nongame species through closed season or license requirements. Thus, the Timber Rattlesnake is protected in these states unevenly, and largely by default. One state in this category, Pennsylvania, lists the snake as a "Candidate Species" for endangered or threatened status, yet paradoxically allows the snake to be taken through sport hunting. Three states (Indiana, Minnesota, Ohio) officially acknowledge concern for the Timber Rattlesnake, or even list it as threatened, but inexplicably provide no legal protection for it. The snake is protected through the state endangered/threatened species listings by eight states, and is listed as extirpated by two (Rhode Island and Maine, the latter without protection). A summary breakdown of the various categories follows:

Legal Protection:

State-listed as an Endangered Species: CT[1], MA[2], NH, NJ, VA[3], VT

State-listed as a Threatened Species: NY[4], TX

State-listed as Extirpated: RI[5]

Protected by Default (partially or fully) as a Closed-season Species, Nongame Species, Non-possession Species, or by other regulation prohibiting or limiting take or sale: AL, AR, GA, IA[6], KS[7], KY, MD, MO, NE, PA[8], SC, TN, VA[3]

Recognition of Concern, but Legal Protection Lacking:
State-listed as a Threatened Species: OH[9]
State-listed as a Special Concern Species: IN, MN
State-listed as Extirpated: ME

Faunal Recognition and Legal Protection Lacking: FL, IL, LA, NC, OK, WV, WI

Further notes on some of the states' actions, as enumerated in the list above, are as follows:

[1]**Connecticut** authorized towns to enact bounties on the Timber Rattlesnake and on the Copperhead, *Agkistrodon contortrix* (Bechtel and Bechtel, 1972), but to my knowledge no bounty system was put in force. Connecticut first prohibited the taking of Timber Rattlesnakes in 1985 *"except that resident landowners or their agents may remove or otherwise dispose of any Timber Rattlesnake found on property owned by them or within a zone designated by the commissioner."* In 1989, Connecticut passed an Endangered Species Law which includes *C. horridus* and provides for the identification of essential habitats for state-listed endangered and threatened species; one assumes the 1985 provision will be overridden once the new law takes effect as expected early in 1992.

[2]In **Massachusetts**, as of 30 August 1991, detailed regulations under a new state Endangered Species Act were promulgated in a public review draft; these regulations provide for the designation of significant habitat for populations of state-listed endangered or threatened species. Legal penalties in Massachusetts are reviewed by French (1992).

[3]In **Virginia,** populations of the canebrake rattlesnake (*Crotalus horridus atricaudatus*) occurring on the coastal plain of the extreme southeastern corner of the state are state-listed as endangered; the listing is only for this taxon, not for the more widely occurring Timber Rattlesnake (*C. h. horridus*) of the Appalachian and Blue Ridge Mountains of northern and western Virginia.

[4]In **New York**, current environmental law does not mandate habitat designation or habitat protection for this or for any state-listed endangered or threatened species. Lacking a legal ability to protect the Timber Rattlesnake's

habitat is a serious deficiency in the current law in New York, and in other states as well (cf. comment 8, below).

[5]**Rhode Island** places *Crotalus horridus* on a list of native species protected against possession and lists it as extirpated (cf. Raithel, 1992).

[6]In **Iowa**, three venomous snake species (*Sistrurus catenatus, Crotalus viridis,* and *Agkistrodon contortrix*) are state-listed as endangered; protection extends to all Iowa snakes except the Common Garter Snake (*Thamnophis sirtalis*) and the Timber Rattlesnake. *Crotalus horridus* has declined to about half of its past recorded Iowa range (Christiansen, 1981).

[7]**Kansas**, in May 1992, officially included *Crotalus horridus* in a special category, Species in Need of Conservation.

[8]**Pennsylvania** allows hunting of Timber Rattlesnakes by licensed sportsmen, but also lists *Crotalus horridus* as a "Candidate Species" defined as *"species which could achieve endangered or threatened status in the future. They are subject to bag and possession limits. A person who catches these species is encouraged to release them immediately and unharmed to the area from which they were taken."* This state thus designates the Timber Rattlesnake's existence as under probable threat, yet at the same time allows it to be hunted. Is this not a contradiction? One might be tempted to ask whether the hunting pressure is perhaps *contributing to* the plight of the snake (see SPORT HUNTING AND ORGANIZED ROUND-UPS above). Like New York, Pennsylvania law does protect state-listed endangered and threatened species but lacks provisions for critical habitat designation for these species.

[9]**Ohio**, in 1990, listed the species as threatened, but without providing for its legal protection.

PRIVATE NATURE PRESERVES

On privately-owned lands in three northeastern states, there are several active management programs underway. Active programs on preserves owned by The Nature Conservancy, or on areas acquired with TNC assistance, are as follows:

Frenchman's Bluff Preserve, New York. Protection, secrecy, patrolling, and vegetation thinning. Contact: Central New York Chapter TNC, 315 Alexander Street, Rochester, New York 14604.

Galick/Bald Mountain Preserve, Vermont. Protection, secrecy, patrolling. Contact: Vermont Field Office TNC, 27 State Street, Montpelier, Vermont 05602.

Loines Preserve, New York. Protection. Contact: Eastern New York Chapter TNC, 1736 Western Ave., Albany, New York 12203.

Meshomasic State Forest, Connecticut. Protection, secrecy, patrolling.

Contact: Sessions Woods Wildlife Management Area, Connecticut Department of Environmental Protection, P. O. Box 1238, Burlington, Connecticut 06013; or Connecticut Chapter TNC, 55 High Street, Middletown, Connecticut 06457.

SUMMARY OF CONSERVATION BIOLOGY

Many populations of *Crotalus horridus* have been exterminated since European colonization of the North American continent, and most remaining denning colonies have been reduced drastically in numbers through bounty hunting, commercial collecting for the exhibit and pet trades, and organized sport hunting. The chief threats today are: (1) habitat destruction, (2) housing developments, (3) sporadic killing or removal, and (4) snake hunting and commercial collecting. The order of importance of these threats varies regionally, but, overall and more than any other factor, human exploitation with its high take of reproductive females has led to the recent depletion or collapse of many populations of *C. horridus*.

In most areas of the Timber Rattlesnake's occurrence, recent surveys of its status show widespread depletion. This finding argues strongly for giving the species complete protection through endangered/threatened listings or closed season regulations. Legal protection, announced and enforced, at state or federal levels, or both, is an important first-step action that, together with management programs, will help the snake's process of recovery.

This species is an irreplaceable component of our native wildlife resources. Its occurrence symbolizes an area's wilderness character. Until recently, the life history of *Crotalus horridus* has remained little studied and poorly documented. Currently, several researchers are actively pursuing long-term field studies which are beginning to build a significant new knowledge of this rattlesnake. A synopsis of these findings follows:

The Timber Rattlesnake is a slow-maturing and long-lived reptile. It has a low reproductive rate. Most females in northern populations do not reach an age of first reproduction until they are nine or ten years old, and they reproduce only at three-year or four-year intervals. Females in northern populations may undertake only three to five reproductive attempts in a lifetime. Reproductive frequency in a population is variable from year to year, the variability effected chiefly by annual climatic vicissitudes. Populations of the Timber Rattlesnake may be characterized generally by little natural "surplus" of individuals, high survivorship of adults, and long-term stability. These demographic traits are the main reasons why recovery of depleted populations will be slow.

In at least one state, Pennsylvania, the snake is "taken" under a licensed sport hunting program, while the neighboring states of New Jersey and New York, like several other northeastern states, offer it protection under state

endangered and threatened species laws. I have presented in detail the case of Pennsylvania to stress that in that state, where the species is still fairly widely distributed, we have a chance to prevent what has happened in the nearby states of New England (extirpation from two, and perhaps imminently from three, states). The snake is currently being harvested at non-sustainable levels in Pennsylvania. Licensed snake hunting as a management tool, as might be applied to a game species, has been a failure as applied to a reptile species with low biological recovery potential. This is a historical lesson that should be straightforward and should heighten our ability to foresee a problem, and to prevent it. Saving the Timber Rattlesnake and promoting its recovery in Pennsylvania certainly will not happen if snake hunting there continues.

The spatial biology and seasonal cycle of the Timber Rattlesnake are centered on its den, where an entire population undergoes communal hibernation through the winter months. The snakes are seasonally migratory, moving away from their dens in spring and back to them in autumn. Maximum migration distances traveled by individual rattlesnakes in a typical northern population average approximately 2.5 miles (4.1 km) in males and 1.3 miles (2.1 km) in females, and can be as long as 4.5 miles (7.2 km). Average seasonal migrations observed in most populations lie within a distance of approximately 1.5 miles (2.4 km) from a den. Males use a home range area of approximately 160–500 acres (65–207 ha), nongravid females 40–100 acres (17–42 ha).

Protecting a viable population of this species depends on protecting the den itself as well as adequate areas of habitat around the den. Protecting an area of 1.5 miles in radius around a den (7 square miles [18 km^2] total area) is recommended as necessary to safeguard a Timber Rattlesnake population. A 1.5-mile radius will protect most females, but may not be adequate for protection of the entire population. A circular area may not be strictly required in all cases, as certain migration directions and elevations may be preferred over others.

In addition to land protection, the main ways to manage and safeguard known populations of this species are:

1. *Protecting* the snake at its known denning colonies through vigilance;
2. *Fencing* in special situations to limit encroachment of private property by rattlesnakes;
3. *Maintaining Secrecy* by not revealing to anyone localities of den sites; reporting sightings to state Natural Heritage Programs;
4. *Avoiding Behavioral Disturbance* of the snakes by restricting or preventing humans from visiting dens and transient habitats;
5. *Patrolling* the area during vulnerable times, particularly (1) the spring emergence period and (2) the summer gestating and birthing periods;
6. *Enhancing Habitat* by vegetation thinning or removing large trees at

some den sites to prevent shading-over and to maintain an open habitat (this technique is somewhat controversial);

7. *Translocating* Timber Rattlesnakes to formerly inhabited den sites (this has never been attempted and should be viewed as experimental);

8. *Restricting Logging* within the summer range of a rattlesnake population and limiting this activity to the winter months;

9. *Removing Nuisance Rattlesnakes* from inhabited areas where the snake may pose a hazard to human safety;

10. *Educating* the public with biologically accurate information, including *emplacement of signs* in areas of occurrence, and working with local residents to promote understanding of the Timber Rattlesnake as a beneficial native species of the deciduous forest community.

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Note on Citations: This bibliography is composed of references to *Crotalus horridus* per se in two groups: (1) Unpublished Reports, Manuscripts, and Abstracts, and (2) Published Literature. Literature citations to papers other than those on *C. horridus* precede the two groups of references on *C. horridus*.

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Figure 1. An adult western-morph male from Houston County, Minnesota, in 1990. Photograph by Barney L. Oldfield.

Figure 2. A subadult western-morph example from Monroe County, Missouri, in 1979. Photograph by Tom R. Johnson.

Figure 3. An adult southern-morph male from LaFourche Parish, Louisiana, in 1988. Photograph by Ernest A. Liner.

Figure 4. An adult yellow-morph female from Washington County, Maryland, in 1992. Photograph by John B. Sealy.

Figure 5. An adult black-morph female from Warren County, New York, in 1991. Photograph by Gerard Lemmo.

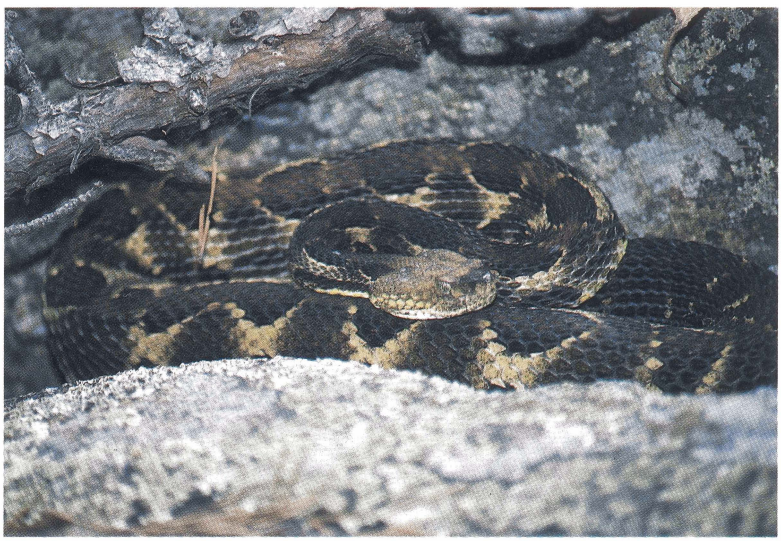

Figure 6. An adult yellow-morph female from Rappahannock County, Virginia, in 1989. Photograph by James Kamstra.

Figure 7. An adult black-morph female from Allegany County, Maryland, in 1992. Photograph by Barney L. Oldfield.

Figure 8. An adult black-morph female from Hampden County, Massachusetts, in 1989. Photograph by Thomas F. Tyning.

Figure 9. An adult western-morph female from Douglas County, Kansas, in 1991. Photograph by Suzanne L. Collins and Joseph T. Collins.

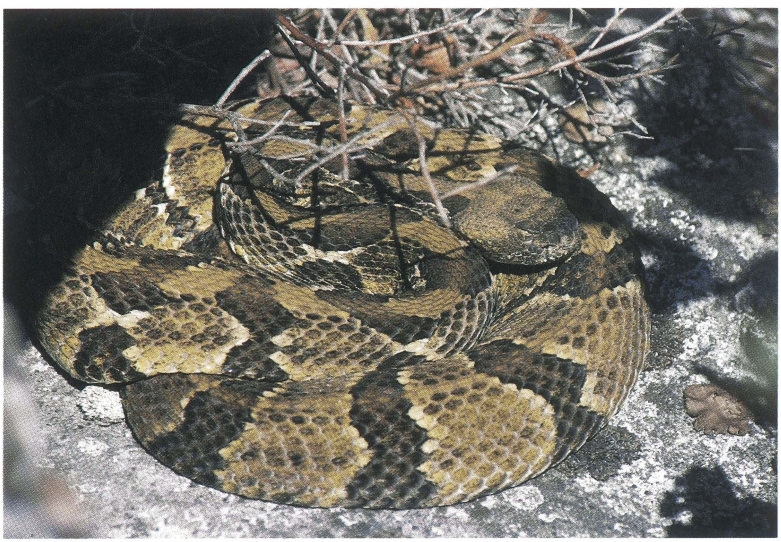

Figure 10. An adult yellow-morph female from Grant County, West Virginia, in 1989. Photograph by James Kamstra.

Figure 11. An adult yellow-morph female from Burlington County, New Jersey, in 1978. Photograph by Robert T. Zappalorti.

Figure 12. An adult yellow-morph female from Ocean County, New Jersey, in 1985. Photograph by Robert T. Zappalorti.

Figure 13. An adult yellow-morph male from Warren County, New York, in 1991. Photograph by Gerard Lemmo.

Figure 14. An adult black-morph example from Schuylkill County, Pennsylvania, in 1991. Photograph by Carl A. Hess.

Figure 15. A newborn yellow-morph example from Warren County, New York, in 1991. Photograph by Gerard Lemmo.

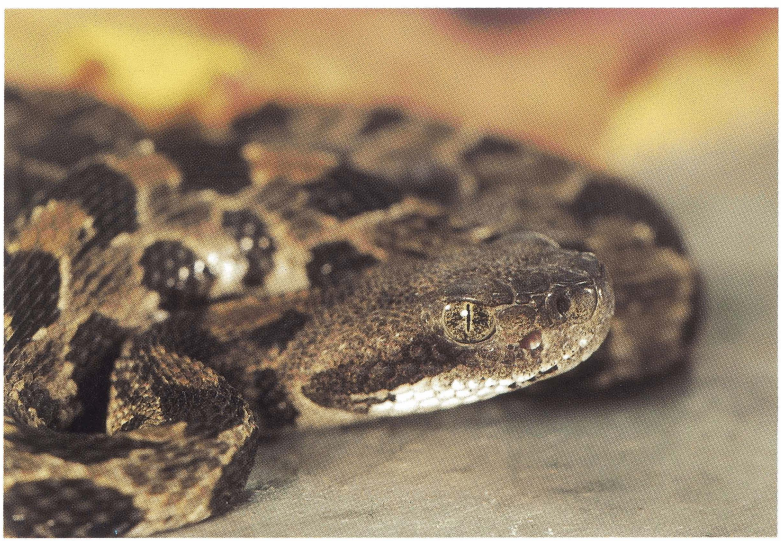

Figure 16. A newborn black-morph example from Warren County, New York, in 1991. Photograph by Gerard Lemmo.

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